Article

Morphology-based phylogenetic analysis of the treehopper tribe Smiliini (Hemiptera: Membracidae: Smiliinae), with reinstatement of the tribe Telamonini

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Abstract

Members of the Smiliini, the nominotypical tribe of the large New World subfamily Smiliinae, are predominately Nearctic in distribution. This tribe included 169 mostly tree-feeding species in 23 genera. A parsimony-based phylogenetic analysis of an original dataset comprising 89 traditional and newly discovered morphological characters for 69 species, including representatives of 22 of the 23 described genera of Smiliini and five other previously recognized tribes of the subfamily, resulted in a single most parsimonious tree with three major clades. The broad recent concept of Smiliini (including Telamonini as a junior synonym) was not recovered as monophyletic by the analysis. Instead, the analysis supported narrower definitions of both Telamonini, here **reinstated** from synonymy, and Smiliini. A key and diagnoses are given to define these tribes, along with discussions of their phylogeny, biogeography, and host plant associations. The genera *Antianthe* Fowler, *Hemicardiacus* Plummer, *Smilirhexia* McKamey, and *Tropidarnis* Fowler are placed as Smiliinae, ***incertae sedis.*** Based on the phylogeny, several genera from both tribes including *Atymna* Stål, *Cyrtolobus* Goding, *Heliria* Stål, and *Telamona* Fitch are not monophyletic.

Diagnostic characters emphasizing the morphological differences between the Smiliini and Telamonini include the dorsal margin of the head, the shape of the pronotum, the size of the pronotal humeral angles, the presence or absence of pronotal longitudinal rugae, the size of forewing cells, variations in the fusion of veins R and M apically in both the fore- and hind wing, and the shape of the apex of the female second valvulae.

Mapping geographic distribution onto the phylogeny suggests that the common ancestor of the ingroup (all three clades) occurred in Central America and Mexico, with multiple dispersals to temperate North America. Many Smiliini and Telamonini feed on various species of oak (*Quercus*) and the close evolutionary association between these insects and their hosts is discussed.

Key words: Homoptera, oak, geographic distribution, biogeography, host plants

Introduction

Treehoppers, or membracids, are intriguing sap-feeding insects found in temperate and tropical regions worldwide. They are well known for their diverse thoracic shapes and distinctive ecological and behavioral traits which include ant-attendance, subsocial behavior, and substrate-borne acoustic communication (Wood 1993; Cocroft and Rodríguez 2005). The over 3000 species of treehoppers are classified into 9 subfamilies and 49 tribes, the largest being the only cosmopolitan subfamily, the Centrotinae (Wallace and Deitz 2004). The New World treehopper subfamily Smiliinae Stål 1866, second only to the Centrotinae in size, includes 82 genera placed in 9 tribes (McKamey 1998). The Smiliinae are characterized by forewings that are partially concealed by the pronotum (Fig. 3B, 1) and by the fusion of forewing veins R_{4+5} and M_{1+2} before the wing apex (Fig. 7A, 1) (Deitz 1975). Most of the recent comprehensive taxonomic research on Smiliinae has focused on the tribes Acutalini (Sakakibara 1997), Amastrini (Evangelista and Sakakibara 2007), Ceresini (Andrade 2004), Micrutalini (Sakakibara 1999), and Polyglyptini (Sakakibara 1996), although Cast (2002), in his Master's thesis, conducted a phylogenetic analysis of the Smiliinae using four mitochondrial genes.

The nominotypical tribe of the Smiliinae, the Smiliini Stål 1866 (*sensu lato*: Deitz 1975; McKamey 1998, 2008), is a predominantly Nearctic group of mainly tree-feeding membracids. Most Smiliini are documented as monophagous, solitary, univoltine, and rarely ant-attended (Wood 1984, 1993; Cast 2002). The tribe contains 169 species (excluding subspecies) in 23 genera (McKamey 1998, 2008) (Table 1). For many years (prior to Deitz 1975), these taxa were separated into two tribes, the Smiliini and the Telamonini Goding 1892. Goding (1892) distinguished genera in the Telamonini from the Smiliini by the number of apical cells in the "wings"—four in Telamonini, the second cell having a truncated base, and three or four in Smiliini, with the second cell having a stylate base (when using "wings," it is assumed Goding was referring to the hind wings, instead using "corium" to refer to the forewings). Additionally, most Telamonini, with a few exceptions, are generally larger in size than Smiliini treehoppers, and have a distinct, constricted pronotal projection or a foliaceous pronotum (Ball 1931; Kopp and Yonke 1974).

Deitz (1975), in his classification of the New World treehoppers, distinguished the Smiliini from other Smiliinae tribes by the separated R, M, and Cu veins at the base of the forewing and the presence of three large sclerotized teeth on the elongated female second valvulae. He also focused on similarities between members of the Smiliini and Telamonini, placing the latter tribe as a junior synonym of the former (see Table 1 for an outline of these classifications). Regarding the traditional key features used to distinguish these tribes, he noted overlap in size (length 3–7 mm in Smiliini, 6–8.5 mm in Telamonini), occasional specimens with "smiliine" hind wing venation in all telamonine genera (Ball 1931), and individuals of the genus *Telamonanthe* with Goding's "smiliine" venation on one hind wing (veins R_{4+5} and M_{1+2} fused and r-m crossvein absent; Fig. 8A, 1) and Goding's "telamonine" venation on the other (R_{4+5} and M_{1+2} free and r-m crossvein present; Fig. 8B, 1). Moreover, Deitz cited similarities in forewing venation, chaetotaxy of the legs, male and female genitalia, and biology (all inhabit and feed exclusively on trees in contrast to members of some other tribes of Smiliinae that feed primarily on herbaceous plants) as evidence supporting this synonymy.

The most recent Smiliini genus and species described was *Smilirhexia naranja* McKamey 2008, from Costa Rica. Only two other species have been described in the last 50 years, *Telamona archboldi* Froeschner 1968, from Florida, and *Cyrtolobus maxinei* Dennis 1970, from Wisconsin. For the purposes of this paper, Smiliini s.l. (*sensu lato*), Smiliini s.s (*sensu stricto*), Smiliini s. Wallace (*sensu* Wallace), Telamonini s.l. (*sensu lato*), and Telamonini s. Wallace (*sensu* Wallace) include the genera listed under these headings in Tables 1 and 2.

Other major taxonomic works on the Smiliini s.s. and Telamonini s.l. include Woodruff (1924) and Ball (1931). Woodruff described many species of *Cyrtolobus*, the largest genus in the Smiliini, and presented numerous useful habitus illustrations of its species. Ball (1931) published a revision of the Telamonini, apparently the first of its kind for treehoppers (Kopp and Yonke 1974), describing 54 species. Dennis (1952) was the first to collectively illustrate the male and female genitalia of various treehoppers from Wisconsin, including the Smiliini s.s. and Telamonini s.l. genera *Cyrtolobus*, *Ophiderma*, *Telamona*, *Thelia*, and *Xantholobus*. Kopp and Yonke (1973a–c, 1974) provided a valuable taxonomic, ecological, and geographical guide to the Smiliini s.s. and Telamonini s.l. with many pronotal illustrations—it is still the most heavily relied upon work for identification of this group today. Quisenberry *et al.* (1978) provided keys to the immatures of the many Smiliini s.l. genera found in Missouri. Wood and Pesek (1992) used discriminate function analysis to characterize the shape of the pronotum of several Smiliini s.l. genera with the goal of elucidating tribal evolutionary relationships.

TABLE 1. Tribes Smiliini and Telamonini as outlined in Metcalf and Wade (1965) vs. Deitz (1975) and McKamey (1998, 2008).

Smiliini Stål 1866 (*sensu stricto*=Metcalf and Wade)[1]	Telamonini Goding 1892 (*sensu lato*=Metcalf and Wade)[2]	Smiliini Stål 1866 (*sensu lato*=Deitz & McKamey)
Antianthe Fowler	*Archasia* Stål	*Antianthe* Fowler
Ashmeadea Goding	*Carynota* Fitch	*Archasia* Stål
Atymna Stål	*Glossonotus* Butler	*Ashmeadea* Goding
Atymnina Plummer	*Heliria* Stål	*Atymna* Stål
Cyrtolobus Goding	*Helonica* Ball	*Atymnina* Plummer
Godingia Fowler[3]	*Hemicardiacus* Plummer	*Carynota* Fitch
Grandolobus Ball[3]	*Palonica* Ball	*Cyrtolobus* Goding
Ophiderma Fairmaire	*Telamona* Fitch	*Glossonotus* Butler
Smilia Germar	*Telamonanthe* Baker	*Godingia* Fowler
Xantholobus Van Duzee	*Telonaca* Ball	*Grandolobus* Ball
--	*Thelia* Amyot and Serville	*Heliria* Stål
--	*Tropidarnis* Fowler	*Helonica* Ball
--	--	*Hemicardiacus* Plummer
--	--	*Ophiderma* Fairmaire
--	--	*Palonica* Ball
--	--	*Smilia* Germar
--	--	*Smilirhexia* McKamey[4]
--	--	*Telamona* Fitch
--	--	*Telamonanthe* Baker
--	--	*Telonaca* Ball
--	--	*Thelia* Amyot and Serville
--	--	*Tropidarnis* Fowler
--	--	*Xantholobus* Van Duzee

[1]= Metcalf and Wade also placed the following genera in the Smiliini, but these were subsequently moved to the Polyglyptini by Deitz (1975): *Adippe* Stål, *Dioclophara* Kirkaldy, *Ennya* Stål, *Gelastogonia* Kirkaldy, *Hemiptycha* Germar, *Heranice* Stål, *Membracidoidea* Goding, *Methesia* Fowler, and *Polyglyptodes* Fowler.

[2]= Metcalf and Wade also placed the following genera in the Telamonini, but these were subsequently moved to the Polyglyptini by Deitz (1975): *Aphetea* Fowler, *Bilimekia* Fowler, *Maturnaria* Metcalf, *Mendicea* Goding, and *Phormophora* Stål.

[3]= Metcalf and Wade erroneously placed these genera in the Telamonini. They were placed in the Smiliini *sensu stricto* in this table based on the classification by Funkhouser (1951).

[4]=New genus, McKamey 2008

More recently, morphological and molecular studies (Dietrich *et al*. 2001a; Cast 2002; Cryan *et al*. 2004) have used Smiliini *s.l.* taxa in their analyses. Dietrich *et al*. (2001a) incorporated *Antianthe*, *Archasia*, and *Smilia* while Cryan *et al*. (2004) sampled *Antianthe* (1 species), *Carynota* (1), *Cyrtolobus* (5), *Glossonotus* (1), *Ophiderma* (5), *Telamona* (2), and *Xantholobus* (1). Cast's (2002) comprehensive examination of the Smiliinae included numerous species and every genus from Smiliini *s.l.* except *Atymnina*, *Godingia*, *Hemicardiacus*, *Palonica*, and *Telonaca*. In addition to providing phylogenies, Cast also hypothesized on the geographic origin of the Smiliini *s.l.* and the close evolutionary relationship with their primary host plant, oak (*Quercus*). The TREEHOPPERS website (Deitz and Wallace 2010) includes photographs (various aspects) of all Smiliini genera, many species, various characters, and keys to the genera of the United States (Wallace 2010). Many workers over the last century have accumulated a vast amount of ecological (e.g. host plant data) and life history data on the Smiliini *s.l.* Some of these include: Funkhouser (1917), Frost (1957), Dennis (1964, 1969), Wood and Olmstead (1984), Wood and Pesek (1992), Wood (1993), Johnson and Freytag (1997), Dietrich *et al*. (1999), Bartlett *et al*. (2008), and Wallace (2008).

TABLE 2. Generic placements based on results of the phylogenetic analysis with approximate numbers of species (excluding subspecies) and known present-day distributions and documented host-plant families and genera. Question marks refer to questionable host plant records. SA=South America, CA=Central America, MX=Mexico, CE U.S.=central and eastern United States, NW U.S.=northwestern U.S., SW U.S.=southwestern United States, CAN.=Canada.

Taxonomic placements as a result of this work (*sensu* Wallace)	Number of species described	Distribution	Host plant genera & families
Smiliini Stål 1866	92		
Ashmeadea Goding	1	MX, SW U.S.	*Quercus* (Fagaceae)
Atymna Stål	10	SA, MX, CE U.S., SW U.S., CAN.	*Castanea, Quercus* (Fagaceae); *Carya* (Juglandaceae); *Vitis* (Vitaceae)
Atymnina Plummer	1	MX	*Quercus* (Fagaceae)
Cyrtolobus Goding	44	MX, CE U.S., SW U.S., CAN.	*Ostrya* (Betulaceae); *Castanea, Fagus, Quercus* (Fagaceae); *Liquidambar* (Hamamelidaceae); *Carya* (Juglandaceae); *Platanus* (Platanaceae)
Godingia Fowler	1	MX	*Quercus* (Fagaceae)
Grandolobus Ball	3	CA, MX, SW U.S.	*Quercus* (Fagaceae)
Ophiderma Fairmaire	17	SA, CA, CE U.S., SW U.S., CAN.	*Castanea, Fagus, Quercus* (Fagaceae); *Pinus* (?) (Pinaceae); *Ulmus* (Ulmaceae)
Smilia Germar	3	MX, CE U.S., SW U.S., CAN.	*Rhus* (Anacardiaceae); *Robinia* (Fabaceae); *Quercus* (Fagaceae); *Carya* (Juglandaceae)
Xantholobus Van Duzee	12	CE U.S., SW U.S., CAN.	*Betula* (Betulaceae); *Quercus* (Fagaceae); *Carya* (Juglandaceae)
Telamonini Goding 1862	68		
Archasia Stål	3	CE U.S., SW U.S., CAN.	*Eupatorium* (?), *Solidago* (?) (Asteraceae); *Robinia* (Fabaceae); *Quercus* (Fagaceae); *Platanus* (Platanaceae); *Malus, Prunus* (Rosaceae); *Verbena* (?) (Verbenaceae); *Vitis* (Vitaceae)
Carynota Fitch	4	CE U.S., SW U.S., CAN.	*Alnus, Betula, Corylus* (Betulaceae)*; Quercus* (Fagaceae); *Hamamelis* (Hamamelidaceae); *Carya, Juglans* (Juglandaceae); *Tilia* (Tiliaceae)
Glossonotus Butler	5	CE U.S., NW U.S., SW U.S., CAN.	*Betula, Corylus* (Betulaceae); *Robinia* (Fabaceae); *Castanea, Quercus* (Fagaceae); *Carya* (Juglandaceae); *Chaenomeles, Crataegus, Malus, Pyrus, Rosa* (Rosaceae); *Vitis* (Vitaceae)
Heliria Stål	11	MX, CE U.S., NW U.S., SW U.S., CAN.	*Fagus, Quercus* (Fagaceae); *Liquidambar* (Hamamelidaceae); *Crataegus, Malus, Prunus, Pyrus* (Rosaceae); *Populus, Salix* (Salicaceae); *Celtis* (Ulmaceae)
Helonica Ball	1	CE U.S.	*Quercus* (Fagaceae); *Vitis* (Vitaceae)
Palonica Ball	6	CA, MX, CE U.S., NW U.S., SW U.S., CAN.	*Betula* (Betulaceae); *Quercus* (Fagaceae); *Populus, Salix* (Salicaceae); *Parthenocissus* (Vitaceae)

TABLE 2. (continued)

Taxonomic placements as a result of this work (*sensu* Wallace)	Number of species described	Distribution	Host plant genera & families
Telamona Fitch	31	SA, MX, CE U.S., NW U.S., SW U.S., CAN.	*Carpinus, Corylus, Ostrya* (Betulaceae); *Nyssa* (Cornaceae); *Robinia* (Fabaceae); *Castanea, Quercus* (Fagaceae); *Hamamelis* (Hamamelidaceae); *Carya, Juglans* (Juglandaceae); *Fraxinus* (Oleaceae); *Platanus* (Platanaceae); *Celtis, Ulmus* (Ulmaceae); *Tilia* (Tiliaceae); *Parthenocissus, Vitis* (Vitaceae)
Telamonanthe Baker	3	CE U.S., SW U.S.	*Quercus* (Fagaceae)
Telonaca Ball	2	CE U.S., SW U.S.	*Quercus* (Fagaceae)
Thelia Amyot and Serville	2	CE U.S., NW U.S., SW U.S., CAN.	*Robinia* (Fabaceae); *Malus, Prunus* (Rosaceae); *Salix* (Salicaceae); *Parthenocissus* (Vitaceae)
Smiliinae, *incertae sedis*	9		
Antianthe Fowler	6	SA, CA, MX, CE U.S., SW U.S.	*Verbesina, Vernonia* (Asteraceae); *Erythrina* (Fabaceae); *Persea* (Lauraceae); *Coffea* (Rubiaceae); *Acnistus, Capsicum, Cestrum, Nicotiana, Solanum* (Solanaceae)
Hemicardiacus Plummer	1	CA	*Quercus* (Fagaceae)
Smilirhexia McKamey	1	CA	no host records
Tropidarnis Fowler	1	MX, SW US	*Quercus* (Fagaceae)

Deitz's (1975) classification of New World treehoppers, which focused on higher-level relationships, included all 22 genera of Smiliini *s.l.*, but only 25 species. Phylogenetic analyses by Dietrich *et al.* (2001a) and Cryan *et al.* (2004) included Smiliini *s.l.* taxa, but in limited numbers (see above). Cast's (2002) large (but unpublished) phylogenetic analysis of the Smiliinae used mitochondrial genes and did not incorporate morphology. Furthermore, despite the biological and ecological fascination with Smiliini treehoppers, the identification of many taxa remains difficult and tedious due to great anatomical variation within and among genera and species. Many of the generic concepts within the group seem poorly defined, plastic, and perhaps artificial, relying historically on the shape of the "pronotal hump." A multitude of taxa in the group show extreme polymorphism in pronotal shape. The need for the present morphology-based phylogenetic analysis including numerous Smiliini *s.l.* species was obvious.

Presented here is the first comprehensive phylogenetic hypothesis of the tribe Smiliini *s.l.* based on morphological characters. This study examined 22 of the 23 genera (*Atymnina* could not be located and was not examined) and 62 total OTUs (species). The objectives were to: research the taxonomic limits of the Smiliini and its included genera; assess the taxonomic validity of Telamonini *s.l.*; infer the evolutionary relationships among the included genera; investigate the historical and new characters defining these taxa (especially the pronotum); and examine patterns in geographic distribution and host plant usage as related to the ancestral origin and phylogeny of these taxa. Phylogenetic analysis also has the potential to highlight "problem taxa" especially in need of taxonomic revision.

Material and methods

Taxonomic sampling. Table 5 lists the taxa (62 species and 29 genera of Smiliinae) included in the analysis indicating their updated tribal placements based on this research. Representatives of all but one of the 23 Smiliini *s.l.* genera were included in the analysis; the genus *Atymnina* Plummer was not examined. The ingroup comprised 52 identified Smiliini species, 3 unidentified Smiliini species, 2 Polyglyptini species, and 1 species each from the

tribes Amastrini, Quadrinareini, and Thuridini. The outgroup consisted of two Ceresini species. To lessen overgeneralization of the data, the type species of all genera but two (*Smilia* and *Telonaca*) were included in the study. Additional terminal taxa were chosen based on their availability and the relative size of each genus: in genera with more than 5 species, at least 2 species were included; with more than 10 species, at least 3, and with more than 20 species, at least 5 species were included. The outgroup (Ceresini) and other non-Smiliini ingroup taxa (Amastrini, Polyglyptini, Quadrinareini, and Thuridini) were selected based on their relatedness to the Smiliini *s.l.* according to the phylogenies presented by Dietrich *et al.* (2001a) and Cryan *et al.* (2004). The Ceresini were chosen to root the tree in the phylogenetic analysis while representatives from the latter four tribes were included to help test the monophyly of the Smiliini.

Characters. Comparative analysis of adult specimens resulted in 89 characters (67 binary and 22 multistate) from the head, thorax (wings and legs), and abdomen (primarily male and female genitalia) (Table 3). Immatures were not examined for this analysis due to the scarcity of authoritatively identified specimens for most species. The following illustrations by Deitz (1975) were used to help code the wings, legs, and genitalia of several specimens that were damaged, missing, or ambiguous: wings—fig. 25f, *Quadrinarea u-flava* Goding; fig. 26g, *Idioderma virescens*; fig. 26i, *Ceresa vitulus*; fig. 26l, *Thuris fenestratus*; fig. 27d, *Hemicardiacus saundersi*; fig 27f, *Atymnina elongata* Plummer; fig. 28b, *Heranice excisata* Schmidt; fig. 28m, *Bryantopsis ensigera*; metathoracic legs—fig. 30a, *C. vitulus*; fig. 30c, *T. fenestratus*; fig. 30d, *Q. u-flava*; second valvulae—fig. 34h, *C. vitulus*; fig. 35c, *I. virescens*; fig. 35o, *Godingia guerreroensis*; fig. 35p, *A. elongata*; fig. 36b, *H. miltoglypta*; fig. 36l, *B. ensigera*; fig. 36t, *T. fenestratus*; fig. 36u, *Q. u-flava*.

All characters were treated as unordered because polarizations were ambiguous and assigned equal weight in the analyses. Question marks (?) in the data matrix indicated missing data and inapplicable character states. Characters in italics in the character list (Table 3) were ultimately excluded from the analysis because they were parsimony uninformative. Character 90, geographic distribution, was also not used in the phylogenetic analysis. See Table 4 for the data matrix of character states. Morphological terminology primarily follows Deitz (1975), Dietrich *et al.* (2001a), and Wallace and Deitz (2004).

TABLE 3. Morphological characters and states used in the phylogenetic analysis of the Smiliini *s.l.* Characters in italics were excluded in the analysis because they were parsimony-uninformative. Character 90, geographic distributions, was mapped onto the tree *aposteriori* and was not used in the phylogenetic analysis.

HEAD:
1. Frontoclypeus inferior margin from anterior aspect: 1, appearing carinate, without ventral projection (Fig. 12B, 1); 2, with ventral projection (Fig. 12C, 1)
2. Proboscis, length of segments: 1, apical and penultimate segment approximately equal in length (proboscis appearing short); 2, apical segment noticeably shorter than penultimate segment (proboscis appearing long) (Fig. 6B, 1)
3. Ocelli: 1, closer to each other than compound eyes (Fig. 6C, 2); 2, roughly equidistant to each other and compound eyes (Fig. 6D, 1); 3, distinctly closer to eyes than each other
4. Dorsal margin: 1, straight or very slightly curved (6D, 2); 2, with abrupt rise near eyes (Fig. 6C, 1)

THORAX:
Pronotum
5. Lateral supraocular callosities: 1, with complete, mostly unbroken band (dark or light) (Fig. 12B, 2); 2, incomplete, broken, appearing spotted (Fig. 6A, 2); 3, represented by a single maculation
6. Antero-lateral vitta: 1, absent; 2, present and distinct (in at least one sex) (Fig. 3D, 3)
7. Anterior oblique vitta: 1, absent; 2, present and distinct (in at least one sex)
8. Anteapical vitta: 1, absent; 2, present (in at least one sex) (Fig. 3C, 2)
9. Dorsal translucent area: 1, absent; 2, present (in at least one sex) (Fig. 3G, 1)
10. Median carina: 1, absent (entire pronotum convex) (Fig. 3F); 2, present on at least portion of pronotum (Fig. 3G) [Coding state 1 makes characters 11-13 inapplicable.]
11. Median carina, length: 1, complete, extending length of pronotum (Figs. 3G; 4A, 1); 2, incomplete, often restricted to horn or projection (Fig. 4F, 2)
12. Median carina, dark pigmentation: 1, absent; 2, present (Fig. 4A, 1)
13. Paired posterior impressions with separating ridge: 1, present (Fig. 3G, 2); 2, absent (Fig. 3F, 1)
14. Large semicircular lateral impression: 1, present (Fig. 3A, 2); 2, absent
15. Overall shape, relative to the degree of pronotal height: 1, low, convex, medially elevated, or with distinct projection; 2, highly elevated and foliaceous (Fig. 4A)
16. Shape of dorsal surface from lateral aspect: 1, flat (Fig. 3D, 1); 2, not flat (including rounded, sinuous, or with distinct pro-

jection) (Fig. 4A)

17. Median anterior horn or projection: 1, absent (Fig. 4A); 2, present (Fig. 4E, 1) [Coding state 1 makes characters 18-27 inapplicable.]
18. Median anterior horn or projection pigmentation: 1, no distinct difference in pigmentation between anterior and posterior areas (Fig. 4D); 2, distinct difference in pigmentation between anterior and posterior areas (anterior often lighter) (Fig. 4E)
19. Median anterior horn or projection anterior inflation: 1, present (Fig. 5C, 1); 2, absent (Fig. 5D)
20. Median anterior horn or projection texture: 1, smoothly textured without a deep fovea at base of projection; 2, highly rippled with distinct fovea at base of projection
21. Median anterior horn or projection (overall shape): 1, narrow, horn-like (Fig. 4D, 1); 2, wide, quadrate or columnar (Fig. 5A-C, E, F) [Coding state 1 makes characters 23-25 inapplicable and coding state 2 makes character 22 inapplicable.]
22. *Median anterior horn length: 1, short; 2, long*
23. Median anterior quadrate/columnar projection, overall shape: 1, quadrate or rounded (Fig. 5A); 2, columnar (Fig. 4E, 1)
24. Median anterior quadrate/columnar projection, posterior slope: 1, posterior slope not gradual, steep and angular (Fig. 5B, 2); 2, posterior slope gradual (Fig. 4E, 2)
25. Median anterior quadrate/columnar projection, shape of dorsal margin: 1, marginate (Fig. 5E, 1); 2, scalloped (Fig. 5B, 1); 3, wavy, or with distinct step (Fig. 5F, 1) [The features in state 3 were combined into one character due to the considerable polymorphism sometimes seen in this feature among conspecific taxa.]
26. Median anterior horn or projection apex with narrow rounded lobe: 1, absent (Fig. 5E, 1); 2, present (Fig. 4D, 1)
27. Median anterior horn or projection with lateral apical compression: 1, present (Fig. 4F, 1); 2, absent
28. Pronotal apex location: 1, anterior to or near humeral angles (Fig. 5D, 1); 2, posterior to humeral angles (Fig. 5B, 1); 3, posterior pronotum (Fig. 3E, 1)
29. *Large postero-lateral swelling: 1, absent; 2, present*
30. Longitudinal rugae: 1, absent or indistinct (Fig. 4A); 2, present and distinct (Fig. 5A, 1) [Coding state 1 makes character 31 inapplicable.]
31. Longitudinal rugae, location: 1, posteriorly only (Fig. 5A, 1); 2, extending entire length of pronotum
32. Humeral angles: 1, not enlarged (Fig. 6D, 3); 2, enlarged (Fig. 6A, 1) [Coding state 1 makes character 33 inapplicable]
33. Humeral angles, enlarged: 1, somewhat rounded apically, slightly enlarged (Fig. 6C, 3); 2, distinctly triangular and stout, enlarged (Fig. 6A, 1); 3, greatly enlarged, long, often narrowed, with anterior margin contacting lateral margin of eye (Fig. 12A, 1)
34. Pubescence: 1, absent or very sparse; 2, present, dense and distinctly erect (Fig. 3D, 2)

Forewing

35. Pigmented spot on apical margin: 1, absent (Fig. 3A); 2, present and distinct (Fig. 3C, 3)
36. Sclerotization in basal half: 1, no heavier immediately anterior than posterior to vein Cu (Fig. 7A); 2, heavier anterior than posterior to vein Cu (Fig. 7D, 1)
37. Degree that wing is concealed by pronotal posterior process: 1, wing not concealed (Fig. 3A, 1); 2, wing partially concealed (Fig. 3B, 1)
38. Spacing of veins: 1, veins crowded anteriorly without large cells separating them, often parallel (Fig. 7B); 2, veins relatively equally spaced with large cells separating them, not parallel (Fig. 7A)
39. Vein R initial division: 1, R_1 and R_S; 2, R_{1+2+3} and R_{4+5} (Fig 7A)
40. Veins R and M: 1, free basally (Fig. 7A); 2, confluent to near mid length of wing, m-cu$_1$ longer than section of M between R and m-cu$_1$; 3, confluent to near midlength of wing, m-cu$_1$ shorter than section of M between R and m-cu$_1$
41. Veins R and M, apical fusion: 1, not confluent preapically; 2, R_{4+5} confluent with M_{1+2} distad of or at beginning of M fork (Fig. 7B, 1); 3, R_{4+5} confluent with M basad of M fork (Fig. 7A)
42. Crossvein m-cu$_1$: 1, present (on at least one wing) (Fig. 7A); 2, absent (Fig. 7C, 1)

Hindwing

43. Veins R_{4+5} and M_{1+2}: 1, free, or if fused, for very short distance (crossvein r-m almost always present) (Fig. 8B, 1); 2, confluent for great distance (crossvein r-m absent) (Fig. 8A, 1)
44. Vein A: 1, branched; 2, unbranched

Legs

45. Shape (primarily meso- and metathoracic): 1, long and cylindrical; 2, short and flattened (Fig. 9A, 1)

Mesothoracic leg

46. Coxal process: 1, not obviously acute, rounded; 2, distinctly acute (Fig. 9B, 1) [Coding state 1 makes character 47 inapplicable]
47. Acute coxal process: 1, short and broad point (Fig. 9B, 1); 2, longer and narrow
48. *Femur ablateral and adlateral cucullate setae: 1, present; 2, absent*

Metathoracic leg

49. Femur ventral ablateral cucullate seta: 1, absent; 2, present (Fig. 9C, 1)
50. Tarsomere I plantar cucullate setae: 1, absent (Fig. 9D, 1); 2, present (Fig. 9E, 1)
51. Tarsomere I apical cucullate setae: 1, 0–2 setae; 2, 3–4 setae (Fig. 9E, 2); 3, 5 or more setae
52. Tarsomere I large apical setae: 1, absent; 2, present
53. Tarsomere II apical cucullate setae: 1, absent (Fig. 9F, 1); 2, present (Fig. 9E, 3)
54. Tibia setal row I: 1, simple row or absent (Fig. 12D); 2, irregular or double row (Fig. 13B)
55. *Tibia setal row II: 1, simple row; 2, irregular or double row*
56. Tibia setae row III: 1, simple row; 2, irregular or double row (Fig. 13A)

ABDOMEN
57. Paired dorsal swellings or remnants of swelling: 1, absent; 2, present

FEMALE GENITALIA
58. Second valvulae width: 1, wide; 2, long and narrow (Fig. 10A)
59. Second valvulae undulations: 1, absent; 2, present
60. Second valvulae basal process: 1, absent; 2, present
61. Second valvulae basal teeth: 1, absent; 2, present (Fig. 14F, 2)
62. Second valvulae curvature: 1, not curved (Fig. 14F); 2, curved (Fig. 10C)
63. Second valvulae distal small teeth: 1, absent (Fig. 10C); 2, present (Fig. 10B, 1)
64. Second valvulae distal large teeth: 1, absent; 2, present (Fig. 10C, 1) [Coding state 1 makes characters 65-69 inapplicable]
65. Second valvulae distal large teeth, number: 1, 1–2; 2, 3 or more (Fig. 10C, 1)
66. Second valvulae distal large teeth, shape: 1, nodular; 2, broad
67. Second valvulae distal large teeth, location: 1, not crowded near apex (Fig. 10C); 2, crowded near apex
68. Second valvulae distal large teeth, spacing: 1, relatively evenly spaced (Fig. 10C, 1); 2, middle and apical teeth distinctly closer (Fig. 10A, 2)
69. Second valvulae distal large teeth, with smaller teeth between large teeth: 1, absent; 2, present
70. Second valvulae apex: 1, dorsal and ventral margin converging proximally, acuminate (Fig. 10C, 2); 2, dorsal and ventral margin converging distally, rounded (Fig. 10A, 1)

MALE GENITALIA
71. Pygofer with lateral plate: 1, apparently absent; 2, free distally; 3, entirely free
72. *Lateral plate dorsoapical posterior hook or lobe: 1, absent; 2, present*
73. Lateral plate medial tooth or process: 1, absent; 2, present
74. *Lateral plate ventral lobe: 1, absent; 2, present*
75. Style shank medial margin: 1, small teeth absent or not distinct (Fig. 10E); 2, small teeth present and distinct (Fig. 11A, 2)
76. Style shank with pre-apical broadening: 1, absent (Fig. 10E); 2, present (Fig. 10F, 2)
77. Style clasp, overall shape: 1, unmodified, without curve or tooth; 2, rounded or angled with small recurved tooth (Fig. 10D, 1), shape not visible from posterior aspect; 3, slightly rounded, with large tooth, not strongly recurved (Figs. 10E, 1), shape visible from posterior aspect (Figs. 11B, 1); 4, usually angular, with large, recurved tooth (Fig. 10F, 1), shape not visible from posterior aspect
78. Style, acuminate distally: 1, present (Fig. 10E); 2, absent (acuminate point)
79. Style clasp orientation from posterior aspect: 1, angled laterally (Fig. 14A, 1); 2, vertical (Fig. 14B, 1)
80. Style clasp, sclerotization: 1, lightly sclerotized; 2, highly sclerotized
81. Style clasp, width: 1, not broadened dorsally; 2, broadened dorsally (Fig. 11B, 1)
82. Style clasp, in lateral aspect: 1, smooth, without teeth (Fig. 10E); 2, with one to several teeth or bumps (Fig. 11A, 1)
83. Aedeagus, width (from lateral aspect): 1, not broadened posteriorly, narrow (Fig. 14C); 2, slightly broadened (Fig. 11C); 3, moderately broadened (Fig. 14D); 4, extremely broadened, with distinct posterior protrusion (Fig. 11D)
84. Aedeagus, shape of shaft from posterior aspect: 1, lateral margins parallel or semi-parallel, with no distinct pre-apical constriction; 2, lateral margins distinctly pre-apically constricted, delimiting a dorsal head (Fig. 11E, 1)
85. Aedeagus, teeth on anterior margin: 1, not concentrated in sclerotized area; 2, concentrated in sclerotized area
86. Connective, medial notch: 1, absent (Fig. 11F, 1); 2, present (Fig. 14E) [Coding state 1 makes character 87 inapplicable]
87. *Connective, medial notch (shape): 1, large; 2, shallow and small*
88. Connective, medial projection on anterior edge: 1, absent (Fig. 14E); 2, present (Fig. 11F, 1)
89. Female length, from head to tip of forewing: 1, 6 mm or less; 2, 6.01–8.0 mm; 3, 8.01 mm or greater
90. Geographic distributions: 1, South America; 2, Central America + Mexico + Caribbean; 3, Eastern and central United States and Canada; 4, Southwestern United States; 5, Northwestern United States

Phylogenetic and geographic analyses. Overall, 62 species were coded for 89 morphological characters in the taxonomic database DELTA (Description Language for Taxonomy) version 1.03e (Dallwitz *et al.* 1993, 1999). Phylogenetic analyses were performed in PAUP* (Phylogenetic Analysis Using Parsimony) version 4.0b10 for

Windows (Swofford 2002). The apomorphy list was also generated using PAUP* (Table 6). A heuristic search using the tree-bisection-reconnection routine (TBR) with 100 replicates was performed. The number of changes per branch and Bremer support were used as measures of node support (Table 6). Bremer support was calculated using the "keep" command in PAUP* to generate parsimonious trees longer than the most parsimonious hypothesis. When a node collapsed in the longer trees, the Bremer support value for that node was calculated by subtracting the number of steps in the most parsimonious tree(s) from the number of steps in the longer tree(s).

To investigate the ancestral locality of the Smiliini *s.l.*, geographic distributions (character 90: Table 3) were optimized on the tree topology *a posteriori* using MacClade 4.06 OS X (Maddison and Maddison 2003). To provide a preliminary hypothesis of the history of geographic distributions, geographic regions were arranged in the following character states: 1, South America; 2, Central America, Mexico, or the Caribbean; 3, the eastern and central United States or Canada; 4, the southwestern U.S. (AZ, CA, CO, NM, NV, TX, UT); and 5, the northwestern U.S. (ID, MT, ND, OR, WA, WY). Species used in the analysis were coded for these character states based on geographic information in McKamey (1998), or for unidentified taxa, locality information on specimen labels. For the analysis, no attempt was made to distinguish "northern Mexico from "Mexico" (grouped in Nearctic and Neotropical Region, respectively by McKamey 1998). No Smiliini *s.l.* are recorded from northern Mexico, Alaska, or Hawaii; Amastrini, Ceresini, and Polyglyptini are known from all five regions cited above; Thuridini are known only from South America; and Quadrinareini are known only from the Caribbean (McKamey 1998).

If taxa were present in more than one region (e.g., more than one character state), they were coded as present for each applicable region ("polymorphic"). The geographic locations of species not included in the analysis were included in the coding of the type species (or the chosen species if no type species was available) if the location differed from the type species or other species representatives. This situation occurred in the following genera: *Atymna*, *Cyrtolobus*, *Ophiderma*, *Palonica*, *Smilia*, and *Telamona*. Non-Smiliini *s.l.* species used in the analysis (outgroups, and see taxonomic sampling above) were coded according to the geographic distribution of the tribes they represent. For example, *Spissistilus festinus* was coded as present for all five character states because the tribe Ceresini is known from all five regions represented in the character. Based on examination of the holotypes, *Heliria cornutula* was not recorded as present in Mexico, although coded as present Mexico in McKamey (1998), and *H. mexicana* was only coded for southwestern U.S. and Mexico. Data (Tables 2, 4) reflect published geographic records and not localities from specimens used in the analysis, unless they were unidentified specimens.
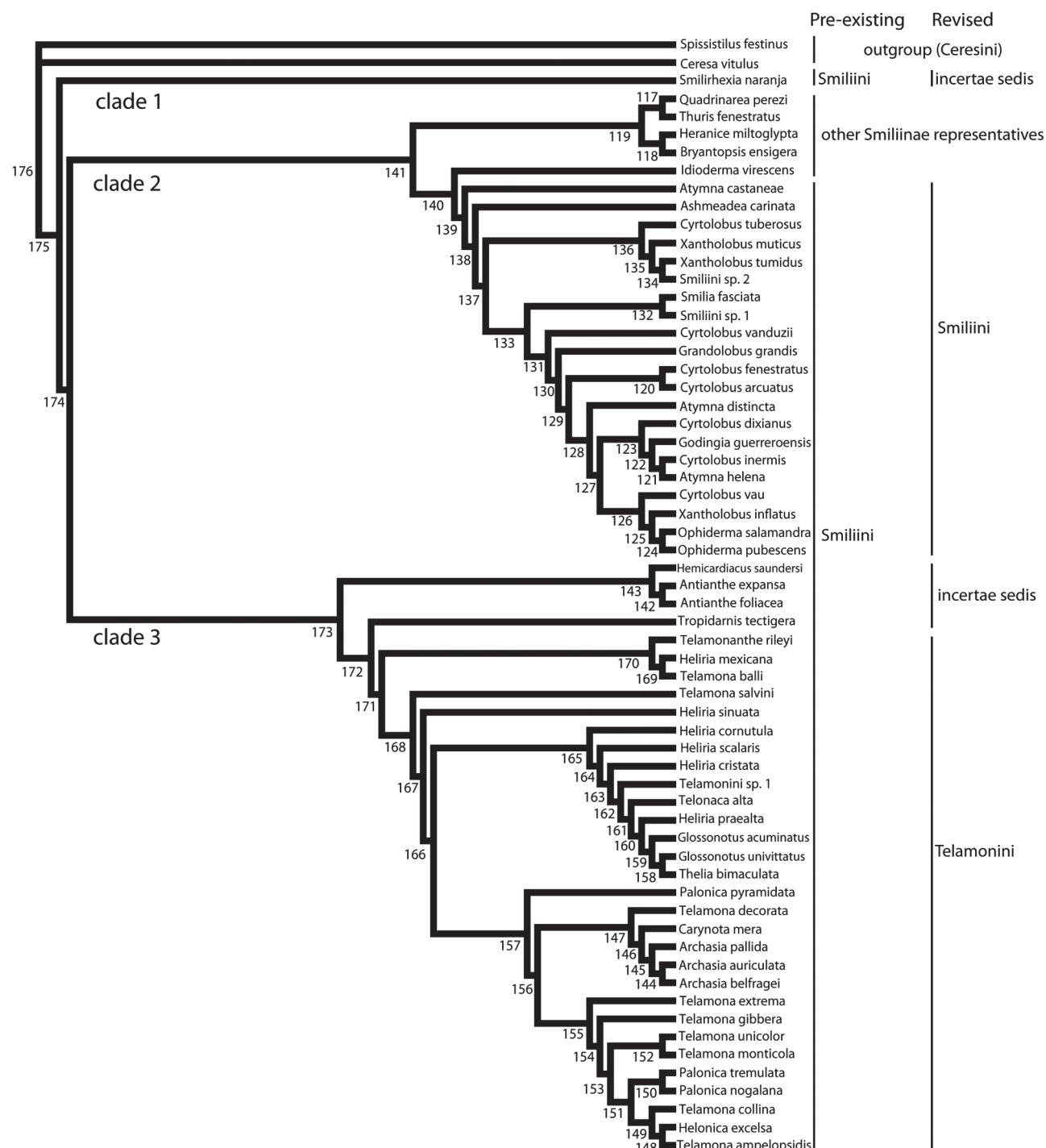
Host plants. Data on host plants and host plant associations for all taxa were gathered from the following sources: Goding (1893); Funkhouser (1917, 1923); Lawson (1922); Woodruff (1924); Ball (1931); Ballou (1935); Osborn (1940); Plummer (1936, 1938); Yothers (1941); Beirne (1961); Dennis (1963, 1964, 1965, 1969); Metcalf and Wade (1965); Kopp (1973 a–c, 1974); Quisenberry *et al.* (1978); Wood and Pesek (1992); Dietrich *et al.* (1999); Wallace *et al.* (2003); Wallace and Troyano (2006); Bartlett *et al.* (2008); Wallace (2008); and USDA (2010).

Results and discussion

The phylogenetic analysis resulted in one most parsimonious tree of 311 steps (Fig. 1), consistency index (CI) of 0.30, and retention index (RI) of 0.77. The ingroup taxa were divided into three major clades: 1), *Smilirhexia naranja*; 2), species representing the Quadrinareini, Thuridini, Polyglyptini, Amastrini, and most Smiliini *s.s.*; and 3), species mostly representing the Telamonini *s.l.*, and *Antianthe*, *Hemicardiacus*, and *Tropidarnis*. Overall, Bremer support for most nodes was low (rarely greater than two) (Table 6), but, nevertheless, many nodes were supported by numerous character changes (e.g., *Smilirhexia*, n=5; 141, clade 2 n=6; 173, clade 3, n=9). The low Bremer support is not surprising when one considers the potentially high amount of unknown lineages—many tropical Smiliini *s.l.* taxa may await discovery. Low support near the tree tips suggests anatomical homogeneity among many species, with very few characters discovered to separate them. Branch support may increase if more characters (including nymphal features) are added to the dataset.

These results render the Smiliini *s.l.* paraphyletic—the genera *Ashmeadea*, *Atymna*, *Cyrtolobus*, *Godingia*, *Grandolobus*, *Ophiderma*, *Smilia*, and *Xantholobus* are more closely related to *Quadrinarea*, *Thuris*, *Bryantopsis*, *Heranice*, and *Idioderma* than other genera in the Smiliini *s.l.*, such as *Archasia*, *Heliria*, and *Telamona*. Moreover, the genus *Antianthe*, originally placed in Smiliini *s.s.*, is grouped with the genus *Hemicardiacus* (Fig. 1). When a monophyletic Smiliini *s.l.* was constrained in PAUP*, it resulted in 100 most parsimonious trees of 315 steps, four
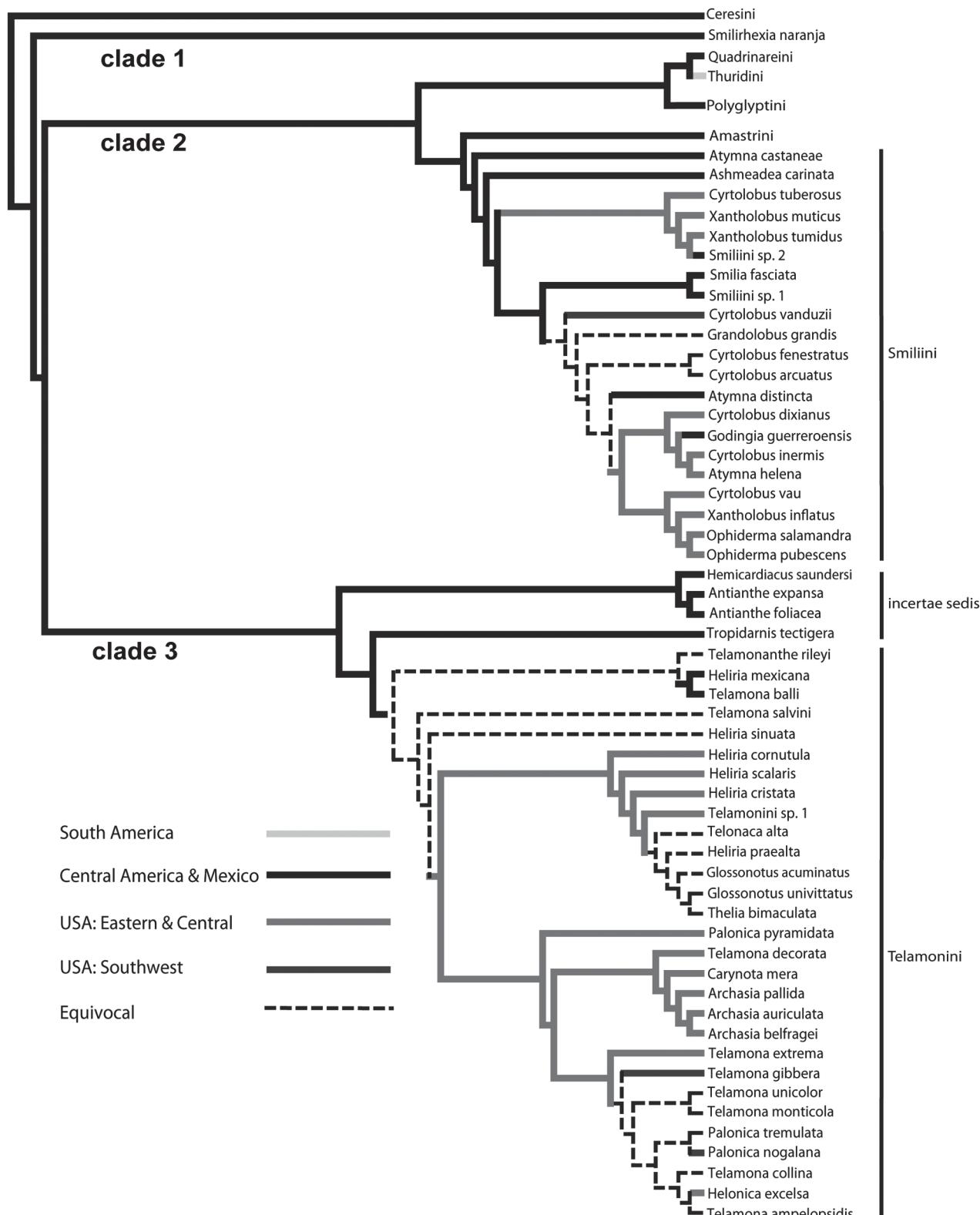
steps longer than the hypothesis presented here. In the constrained analysis, however, the Smiliini *s.s.* and Telamonini *s.l.* were sister groups, providing further evidence for recognizing each as discrete tribes.
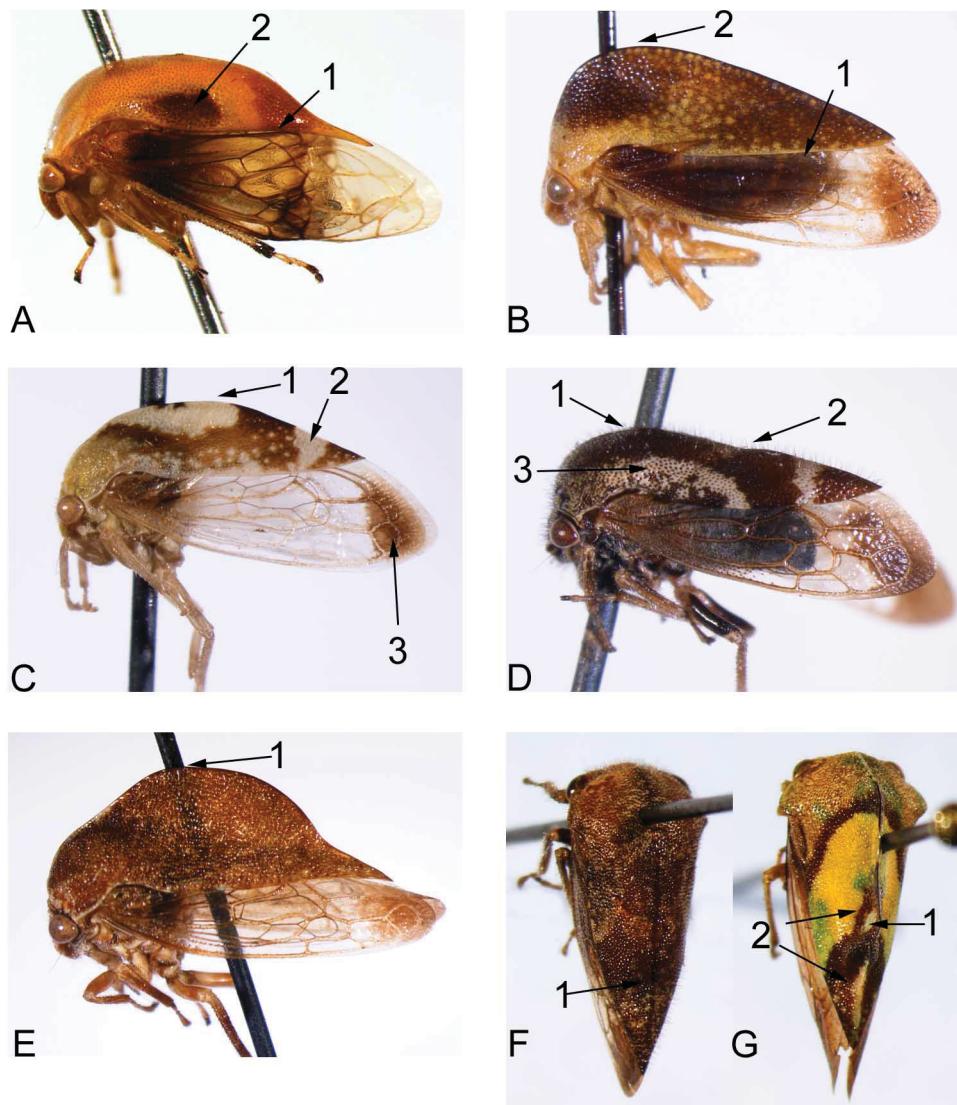
FIGURE 1. Phylogenetic relationships generated from cladistic analysis of the entire dataset, illustrating the new proposed reclassification of the Smiliini *s.l.* Analysis in PAUP* resulted in a single most parsimonious tree with 311 steps. Bremer support and synapomorphies for nodes are listed in Table 6.

All specimens examined from Smiliini *s.l.* had the diagnostic features listed by Deitz (1975): veins R, M, and Cu separate near the base (Fig. 7A) and the female second valvulae elongated with three prominent dorsal teeth (Fig. 10C, 1). These characters, however, did not unite the Smiliini *s.l.* here because the Polyglyptini taxa in the analysis also have veins R, M, and Cu separate near the base and the Ceresini and Amastrini representatives have elongated female second valvulae. The presence of three large teeth on the female second valvulae is largely restricted to the Smiliini *s.l.* observed in the study, but several other non-Smiliini taxa in the analysis were opti-

mized as this character state in PAUP*, as a result of being coded with a "?", due to character inapplicability. Further, Deitz (1975: fig. 35) discovered that the female second valvulae of some non-Smiliini taxa (some Amastrini) have three large dorsal teeth.
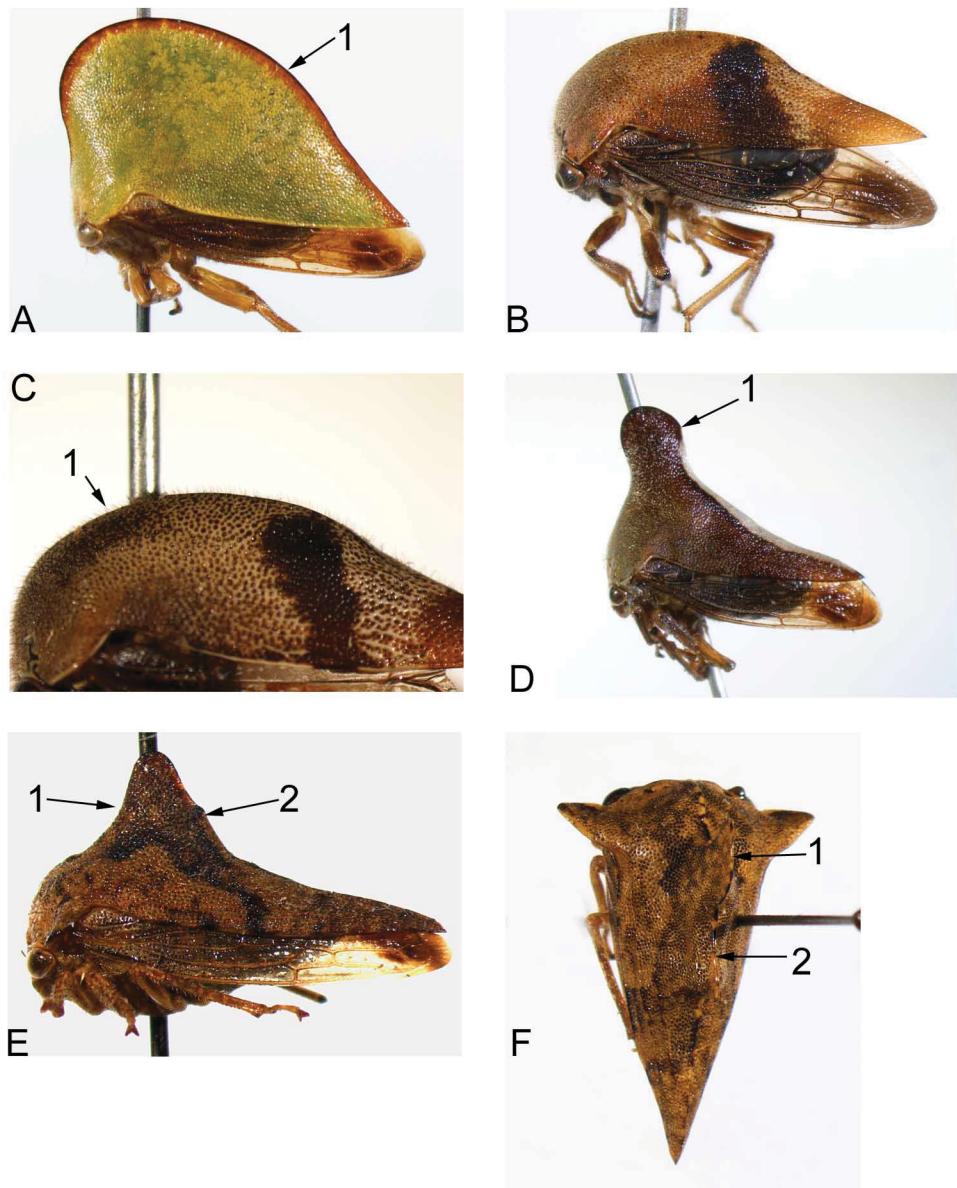
FIGURE 2. Reconstruction of ancestral geographic distributions of the Smiliini *s.* Wallace, Telamonini *s.* Wallace based on present-day distributions (Character 90) (Table 3) as optimized (ACCTRAN) on a phylogeny derived from Fig. 1. See Table 2 for OTU distributions and Materials and Methods for explanations of OTU coding.

FIGURE 3. Selected taxa in lateral and dorsal aspects, and character states in the analysis. A, *Smilirhexia naranja* McKamey, holotype, ♂: 1, forewing not concealed by pronotum; 2, large semicircular lateral impression. B, *Atymna castaneae* (Fitch): 1, forewing concealed by pronotum; 2, pronotal apex near or anterior to humeral angles. C, *A. helena* (Woodruff), #09-175e♂: 1, pronotal peak located posteriorly; 2, anteapical vitta; 3, forewing pigmented spot on apical margin. D, *Ophiderma pubescens* (Emmons): 1, dorsal surface of pronotum flat; 2, pronotal pubescence; 3, antero-lateral vitta. E, *Xantholobus tumidus* (Walker), #09-182d♀: 1, pronotal peak located posteriorly. F, *O. salamandra* Fairmaire: 1, median carina and posterior impressions absent. G, *Smilia fasciata* Amyot and Serville, #09-181c♀: 1, dorsal translucent area; 2, paired posterior impressions with separating ridge.
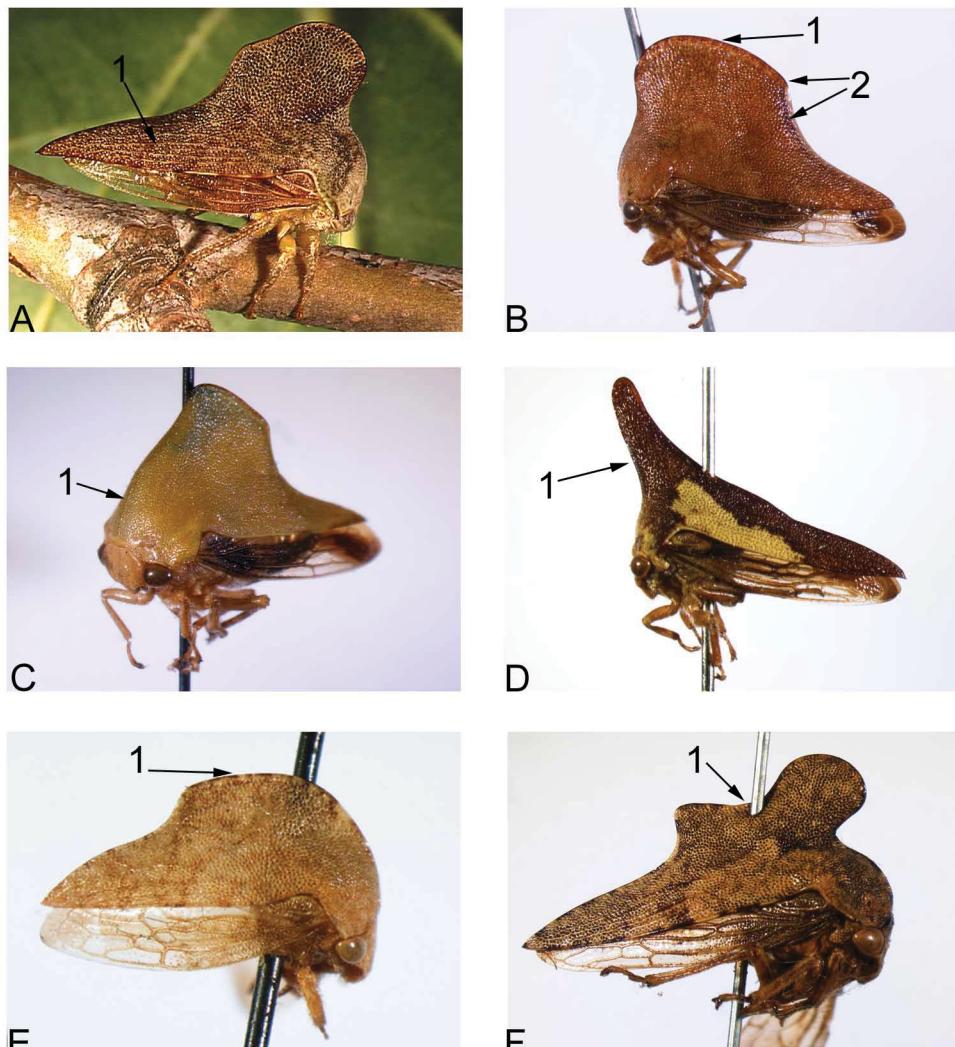
Many anatomical characters support the basal relationships of the phylogenetic tree (Fig. 1). **Clade one**, *Smilirhexia naranja*, was placed in the Smiliini *s.l.* by McKamey (2008) based on its apically fused R and M veins and two m-cu crossveins in the forewing. In several characters, however, this enigmatic species differs from most other taxa in this analysis: the pronotum does not conceal the forewings (Fig. 3A, 1) (like Ceresini); the plantar cucullate setae on metatarsomere I are absent (Fig. 9D, 1); and the pronotum has a large semicircular lateral impression (Fig. 3A, 2) (like many Ceresini). Although *S. naranja* appears to be closely related to the Ceresini and may form its own tribe, it is here placed as Smiliinae, *incertae sedis*. Taxa in **clade two** have R_{4+5} and M_{1+2} veins in the hind wing confluent for a great distance (Fig. 8A, 1) (exception: Smiliini sp. 1) and metathoracic tarsomere II without apical cucullate setae (Fig. 9F, 1). Treehoppers in **clade three** have the following features: an abrupt rise on the dorsal margin of the head (Fig. 6C, 1); enlarged humeral angles (Fig. 6A, 1); forewings with the veins crowded anteriorly and without large cells separating most veins (Fig. 7B); and most species with females large in size, at least 8.01 mm in length.

FIGURE 4. Selected taxa in lateral and dorsal aspects, and character states in the analysis. A, *Archasia belfragei* Stål: 1, median carina extending length of pronotum, with dark pigmentation. B, *Carynota mera* (Say). C, *C. mera*, #09-173f♂: 1, pronotal pubescence present, distinct, and erect. D, *Glossonotus univittatus* (Harris): 1, median anterior horn laterally flattened and with narrow rounded apex. E, *Palonica pyramidata* (Uhler): 1, median anterior horn or projection, columnar in shape; 2, posterior slope of projection gradual. F, *Heliria cristata* (Fairmaire): 1, median anterior projection laterally flattened; 2, median carina restricted to median anterior projection.

Results of other treehopper evolutionary studies including Smiliini *s.l.* taxa both support and challenge these findings. The morphological analysis of the Membracidae by Dietrich *et al.* (2001a) included only three Smiliini *s.l.* genera (*Antianthe*, *Archasia*, and *Smilia*), but they did form an unresolved monophyletic group. In phylogenetic analyses derived from combined morphological and molecular data (Cryan *et al.* 2004), the Smiliini *s.s.* were paraphyletic with respect to a monophyletic Telamonini *s.l.*, similar to the present analysis. Furthermore, some topologies in that study (Cryan *et al.* 2004) revealed a paraphyletic Smiliini *s.l.* with respect to the Polyglyptini, suggesting a close relationship between these tribes, as also demonstrated here (Fig. 1). Both the present study and Cryan *et al.* (2004) show a monophyletic *Ophiderma* and paraphyletic *Cyrtolobus*. The topology of Cryan *et al.* (2004), however, unlike the present analysis, showed some *Cyrtolobus* spp. grouping closely with several Telam-

onini *s.l.* and *Antianthe* grouping with some *Cyrtolobus* spp. and *Ophiderma* spp. These differences may be due to low taxon sampling in the earlier study—only 13 species of Smiliini *s.s.* in 4 genera and 4 Telamonini species were used.
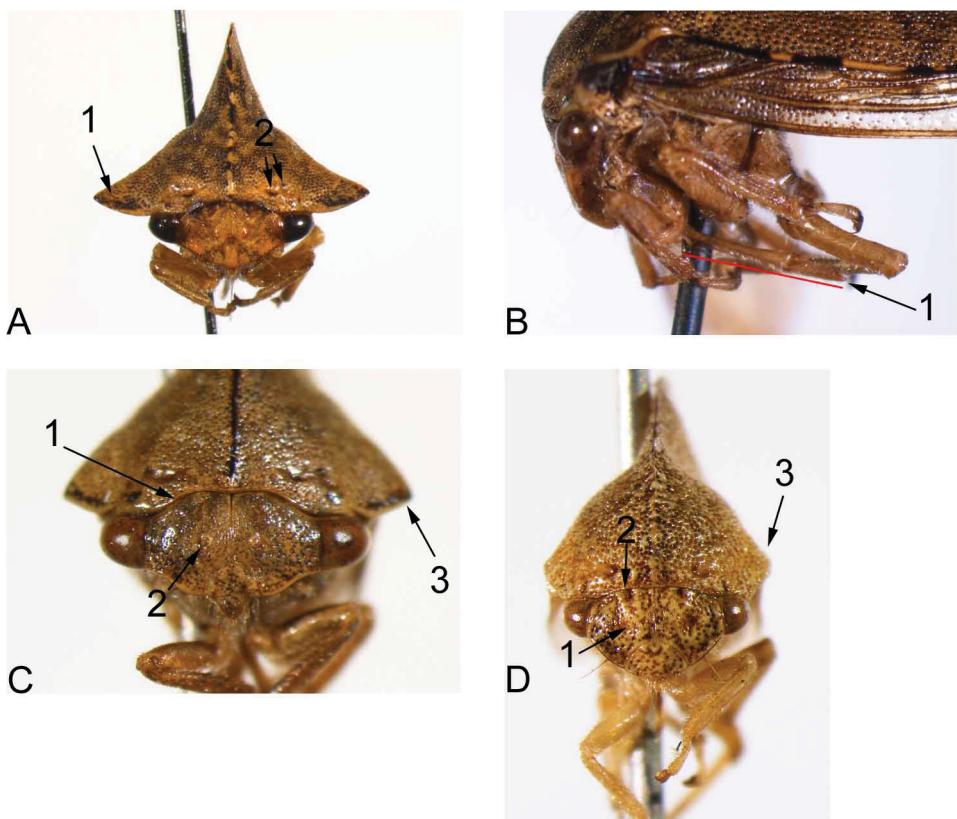
FIGURE 5. Selected taxa in lateral aspects, and character states in the analysis. A, *Telamona collina* (Walker): 1, longitudinal rugae on posterior pronotum. B, *T. extrema* Ball: 1, quadrate projection dorsal margin scalloped and pronotal peak posterior to humeral angles; 2, quadrate projection posterior slope steep and angular. C, *T. unicolor* Fitch: 1, median anterior horn or projection with anterior inflation. D, *Thelia bimaculata* (Fabricius): 1, pronotal apex anterior to or near humeral angles. E, *Telamonanthe rileyi* (Goding), #72-11f♂: 1, quadrate projection dorsal margin marginate. F, *Heliria cristata* (Fairmaire), #72-9d♀: 1, quadrate projection dorsal margin wavy or with distinct step.

The largest previous phylogenetic analysis of the Smiliinae was done by Cast (2002) in his unpublished Master's thesis. Using DNA sequences from four mitochondrial genes, he analyzed 7 of the 9 Smiliinae tribes using parsimony and Bayesian methods. Cast determined that the subfamily Smiliinae and the tribe Smiliini were not monophyletic in both analyses, based on the exclusion of the tribe Micrutalini and the genus *Antianthe*, respectively. In the parsimony trees, the relationships among the Amastrini, Polyglyptini, Smiliini *s.l.* (excluding *Antianthe*), and Tragopini were unresolved, but in the Bayesian tree, the relationships were more defined with Smiliini *s.l.* (excluding *Antianthe*) sister to a large group of Polyglyptini genera, *Vanduzea* sp. (Amastrini), and *Antianthe*. Nonetheless, the non-monophyly of Smiliini *s.l.* and relative uncertainty of the relationships among Amastrini, Polyglyptini, and Smiliini *s.l.* found by Cast, support the findings of this study. Further, in both of Cast's analyses, the tribe Smiliini *s.l.* was divided into two independent monophyletic sister lineages, the Smiliini *s.s.* and Telamonini *s.l.* (each node with 100% node support in the Bayesian analysis), and several genera in both clades were not

monophyletic. Based on these results, Cast suggested that Telamonini be reinstated. More detailed comparisons between Cast's phylogenies and the hypothesis presented here are addressed below in the discussion of lineages.

FIGURE 6. Selected taxa in anterior and lateral aspects, and character states in the analysis. A, *Heliria cristata* (Fairmaire): 1, pronotal humeral angles enlarged, triangular and stout; 2, pronotal lateral supraocular callosities incomplete and broken. B, *H. cristata*, #72-9c♂: 1, apical segment of proboscis noticeably shorter than penultimate segment (proboscis appearing long). C, *Glossonotus univittatus* (Harris): 1, dorsal margin of head with abrupt rise near eyes; 2, ocelli closer to each other than to compound eyes; 3, pronotal humeral angles slightly enlarged and somewhat rounded apically. D, *Cyrtolobus arcuatus* (Emmons): 1, ocelli roughly equidistant to each other and compound eyes; 2, dorsal margin of head straight or very slightly curved; 3, pronotal humeral angles not enlarged.

Wood and Pesek's (1992) analysis of pronotal shape using canonical discriminant analysis revealed three groups of Smiliini: those with highly elevated foliaceous pronota (*Antianthe*, *Archasia*, *Hemicardiacus*, *Smilia*, and *Telamonanthe*), those with elevated/triangular pronota (*Heliria*, *Glossonotus*, *Telamona*, and *Thelia*), and treehoppers with lower pronota (*Atymna*, *Carynota*, *Cyrtolobus*, *Godingia*, *Grandolobus*, *Ophiderma*, and *Xantholobus*). One grouping—*Heliria*, *Glossonotus*, *Telamona*, and *Thelia*—was similar to the present findings. Wood and Pesek's (1992) classification, however, is likely artificial due to the few characters sampled, all from the pronotum.

Dennis (1952) reported, with a few exceptions, that genitalia were relatively unimportant in classifying taxa of Smiliini *s.s.* and Telamonini *s.l.* and that features varied within genera, species, and specimens. Certain characteristics of the male and female genitalia examined in the present study, however, remained consistent among taxa and were extremely useful in delineating major groups of genera. Indeed, Kopp and Yonke (1974) observed the importance of genitalia in classifying Ceresini and their potential usefulness for telamonines as verified in the tribal discussions below.

The present analysis resulted in the generic placements shown in Figure 1 and Table 2, including a redefinition of the tribe Smiliini (now similar to that of Smiliini *s.s.*), the reinstatement of the tribe Telamonini Goding, and the placement of *Antianthe*, *Hemicardiacus*, and *Tropidarnis*, Smiliinae *incertae sedis*. In the remaining text, the new arrangements of the tribes Smiliini and Telamonini are herein referred to as Smiliini *s.* Wallace and Telamonini *s.* Wallace. The hypothesis presented reveals numerous non-monophyletic genera within both Smiliini and Telamonini, demonstrating that current generic concepts require re-analysis and revision.

The following key and diagnostic features below distinguishes these two tribes as defined herein. This key can replace "SMILIINI" in couplet 24 of Deitz's (1975, p.15) "Key to Subfamilies and Tribes of the New World Membracidae," and couplet 31 of Dietrich *et. al's* (2001a, p. 215) "Key to subfamilies, tribes and unplaced genera of New World Membracidae."

1   Head dorsal margin straight or very slightly curved (Fig. 6D, 2); distinct median anterior horn or projection absent (Figs. 3B–D); pronotal longitudinal rugae absent (Fig. 3B); humeral angles not enlarged (Fig. 6D, 3); forewing veins not crowded anteriorly, and with large cells separating them (Fig. 7A); forewing R_{4+5} vein confluent with M vein basad of M fork (Fig. 7A); hind wing with R_{4+5} and M_{1+2} veins confluent for great distance (in some tropical taxa, these veins may be free) (Fig. 8A, 1); dorsal and ventral margins of second valvulae apex converging distally, apex rounded (Fig. 10A, 1); females usually less than 8 mm in length. . . . .*Smiliini s.* Wallace

-    Head dorsal margin with abrupt rise near eyes (Fig. 6C, 1); median anterior horn or projection almost always present (Fig. 5) (absent in *Archasia* and *Carynota*); pronotal longitudinal rugae almost always present (Fig. 5A, 1); humeral angles enlarged (Fig. 6A, 1); forewing veins crowded anteriorly, and without large cells separating them (Fig. 7B); forewing R_{4+5} vein confluent with M_{1+2} vein distad of M fork (Fig. 7B, 1); hind wing with R_{4+5} and M_{1+2} veins free (or if fused, for short distance) (Fig. 8B, 1); dorsal and ventral margins of second valvulae apex converging proximally, apex acuminate (Fig. 10C, 2); females usually 8 mm or more in length . . . .*Telamonini s.* Wallace
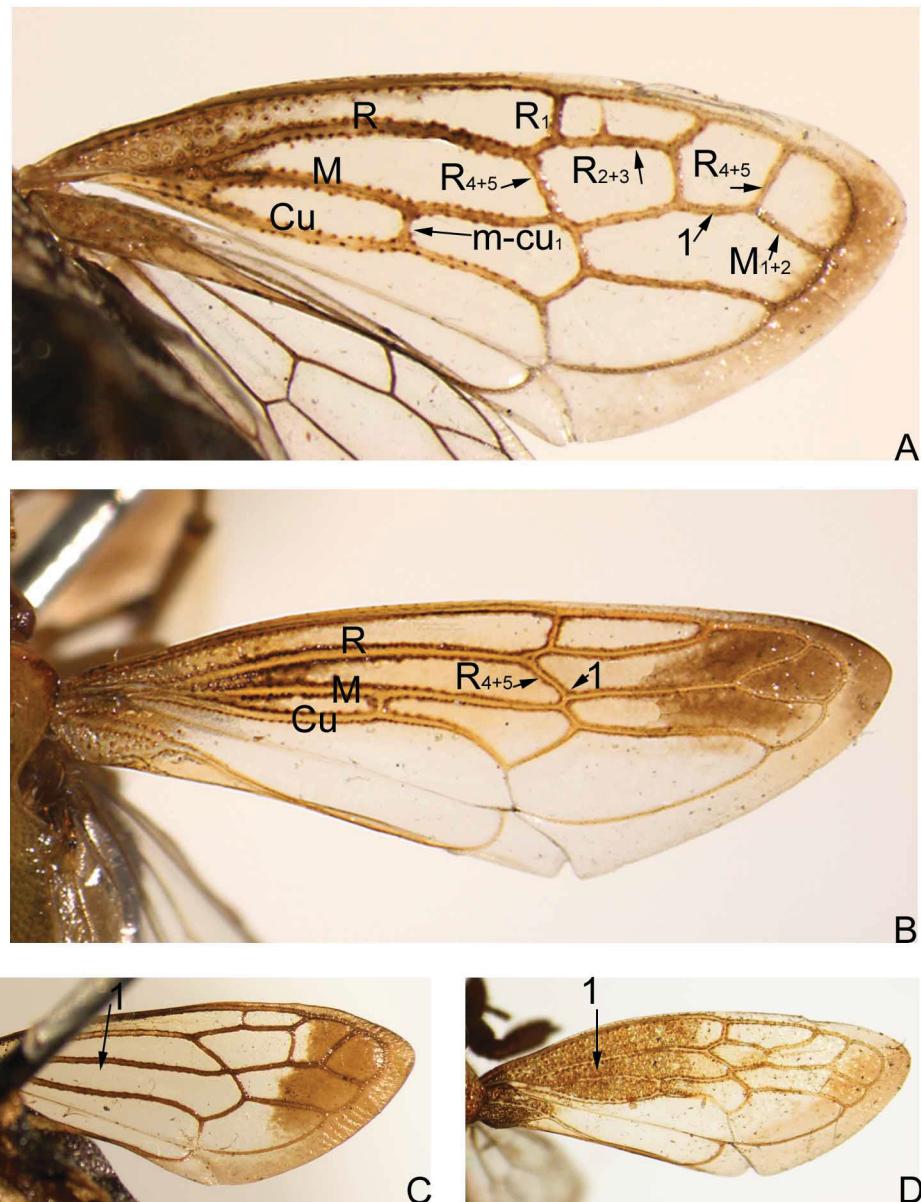
Smiliini Stål 1866 *s.* Wallace

Diagnostic characters. Females usually less than 8 mm in length (except in *Grandolobus*, *Godingia*, *Smilia*, and some *Cyrtolobus* spp., like *C. tuberosus*). Head dorsal margin straight or very slightly curved (Fig. 6D, 2); ocelli equidistant to each other and compound eyes (Fig. 6D, 1). Pronotum highly elevated and foliaceous only in *Smilia* and some *Grandolobus*; without distinct median anterior horn or projection (Fig. 3C, 1); median carina complete (Fig. 3B, 2) (except in *Ophiderma*); longitudinal rugae absent (Fig. 3E); humeral angles not enlarged (Fig 6D, 3). Forewing partially concealed by pronotal posterior process (Fig. 3B, 1); R, M, and Cu veins separate near base; veins not crowded anteriorly, and with large cells separating them (Fig. 7A); R_{4+5} vein confluent with M vein basad of M fork (Fig. 7A). Hind wing with R_{4+5} and M_{1+2} confluent for great distance (Fig. 8A, 1). Metathoracic tarsomere II apical cucullate setae absent (Fig. 9F, 1); tibia with cucullate setal row I irregular or double. Dorsal and ventral margins of second valvulae apex converging distally, apex rounded (Fig. 10B, 1); often with small teeth distally and with the larger middle and apical teeth distinctly closer (Fig. 10A, 2). Male style clasp never angular with a large recurved tooth, either rounded or angled with small recurved tooth (Fig. 10D, 1), or slightly rounded with large tooth not strongly recurved (Fig. 10E, 1); aedeagus width from lateral aspect variable, but never extremely broadened.

Based on the phylogenetic analysis presented, the tribe Smiliini *s.* Wallace is here organized (Fig. 1, Table 2) into a group similar to the classification presented by Metcalf and Wade (Fig. 1, Table 1). Although not examined in this analysis, the genus *Atymnina* is placed in Smiliini *s.* Wallace based on the overall resemblance to the genus *Atymna* as described in Plummer (1938) and characteristics of the forewings and second valvulae, illustrated in Deitz (1975). Despite low Bremer support (1), this group of genera is monophyletic and has two apomorphies supporting it on the phylogeny: vein R initial division R_{1+2+3} and R_{4+5} (Fig. 7A) and the mesothoracic coxal process with a short acute point (Fig. 9B, 1). The long list of diagnostic characters and key above emphasize the differences between this tribe and the Telamonini *s.* Wallace in virtually every body region—the head, pronotum, wings, legs, and male and female genitalia. In his molecular analysis of the Smiliinae, Cast (2002) also recovered a monophyletic Smiliini, which included *Ashmeadea*, *Atymna*, *Cyrtolobus*, *Grandolobus*, *Ophiderma*, *Smilia*, and *Xantholobus*. This group in his study, however, was sister group to the Telamonini, while in the present analysis, these two groups were more distantly related (Fig. 1).

It is premature to combine these Smiliini genera (Table 2) with their relatives (e.g., Amastrini and Polyglyptini) from **clade two** into a taxon, without first including further Smiliinae tribal representatives in an analysis. The low Bremer support and few character changes supporting the Smiliini may be an artifact of the taxa selected to represent the other Smiliinae tribes included in the analysis. That is, some features historically used to characterize the Smiliini *s.s.* may be shared convergently with other taxa (e.g. *Quadrinarea*, *Bryantopsis*, and *Idioderma*) and not with the Telamonini *s.* Wallace or with other treehoppers from the Amastrini and Polyglyptini not sampled here. For instance, the fused R_{4+5} and M_{1+2} veins (Fig. 8A, 1) in the hind wing is a synapomorphy for **clade two** (with
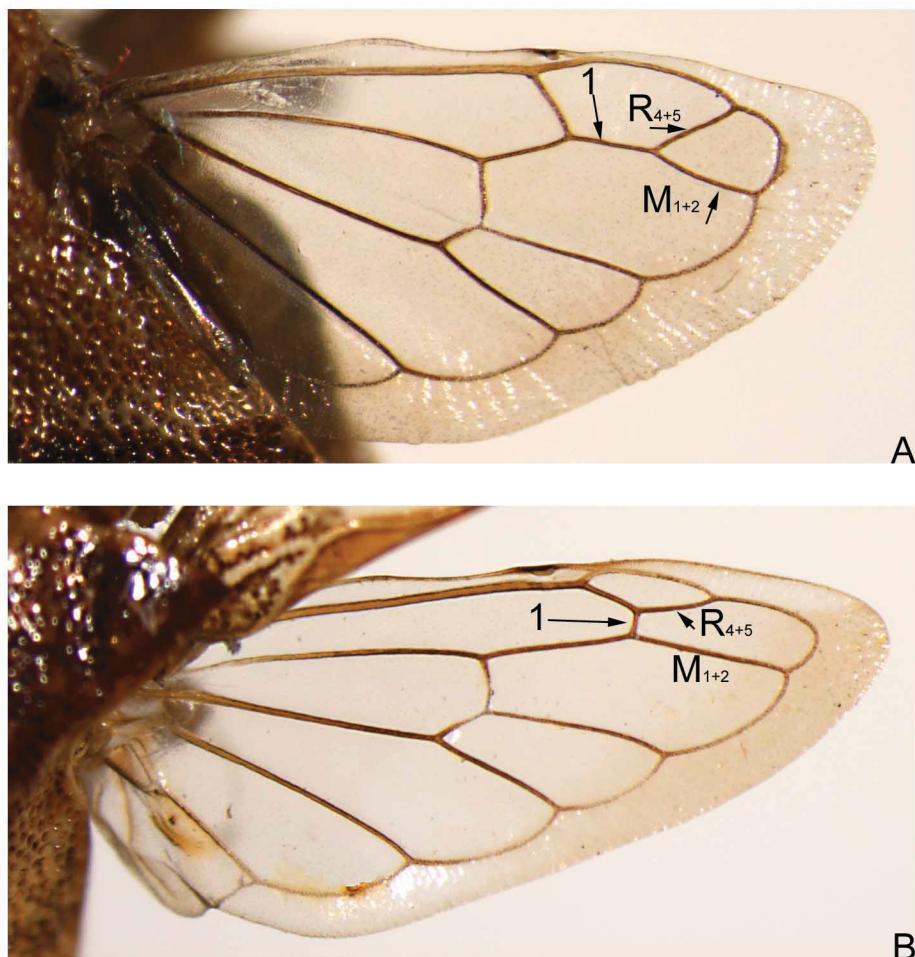
only one reversal) but had also been used to differentiate the Smiliini *s.s.* from other Smiliinae tribes (Goding 1892). Some Polyglyptini genera not included in the analysis, however, show a variation in this hind wing state: veins R_{4+5} and M_{1+2} in the hind wing are fused, but not diverging apically (Deitz 1975: fig. 29 d, g). Further, the clade *Idioderma* (Amastrini representative) + (Smiliini *s.* Wallace) (Bremer support=2) is supported by the apically converging dorsal and ventral margins of the female second valvulae, forming a rounded tip (Fig. 10A, 1). This feature, however, does not appear to be consistent among all Amastrini genera (Deitz 1975). So, the inclusion of additional Smiliinae taxa in future analyses may result in increased support for Smiliini *s.* Wallace by the revealing of unique synapomorphies.

FIGURE 7. Selected forewings and character states in the analysis. A, *Cyrtolobus fuliginosus* (Emmons), right forewing: 1, apical fusion of veins R and M. B, *Archasia belfragei* Stål, right forewing: 1, vein R_{4+5} confluent with vein M_{1+2} distad of M fork. C, *Smilia camelus* (Fabricius), right forewing, #09-160g♂: 1, crossvein m-cu$_1$ absent. D, *Telamonanthe rileyi* (Goding), left forewing (inverted), #72-11f♂: 1, sclerotization in basal half wing heavier anterior than posterior to vein Cu.

In the analysis (Fig. 1), the Smiliini *s.* Wallace are composed of two basal lineages consisting of single taxa (*Atymna castaneae* and *Ashmeadea carinata*), a clade including *Cyrtolobus tuberosus* and several *Xantholobus* spp., and a large clade including *Grandolobus, Godingia, Ophiderma, Smilia*, and various *Atymna* and *Cyrtolobus* species. The sister group to *Ashmeadea carinata*, which includes most Smiliini *s.* Wallace, is typified by a slightly

broadened aedeagus, when viewed laterally (Fig. 11C). The first major clade (containing *C. tuberosus*) is supported by three character changes, notably the apex of the pronotum located centrally (Fig. 3E, 1) and the aedeagus with a distinct apical head when viewed posteriorly (Fig. 11E, 1). The rounded or angled male style clasp with a small recurved tooth (Fig. 10D, 1) and small medial projection on the connective (Fig. 11F, 1) found in this group are also seen in closely related taxa (e.g. *Atymna castaneae*, *Ashmeadea carinata*, *C. vanduzii*, and *Smilia fasciata*). Dennis (1952) first documented the small medial projection on the connective as a feature that characterized the genus *Xantholobus*. Cast (2002) also discovered a close relationship between *C. tuberosus*, *C. vanduzii*, and *Smilia* in his Bayesian analysis of the Smiliini *s.s.* —they formed a monophyletic group along with two southwestern *Ophiderma* species.
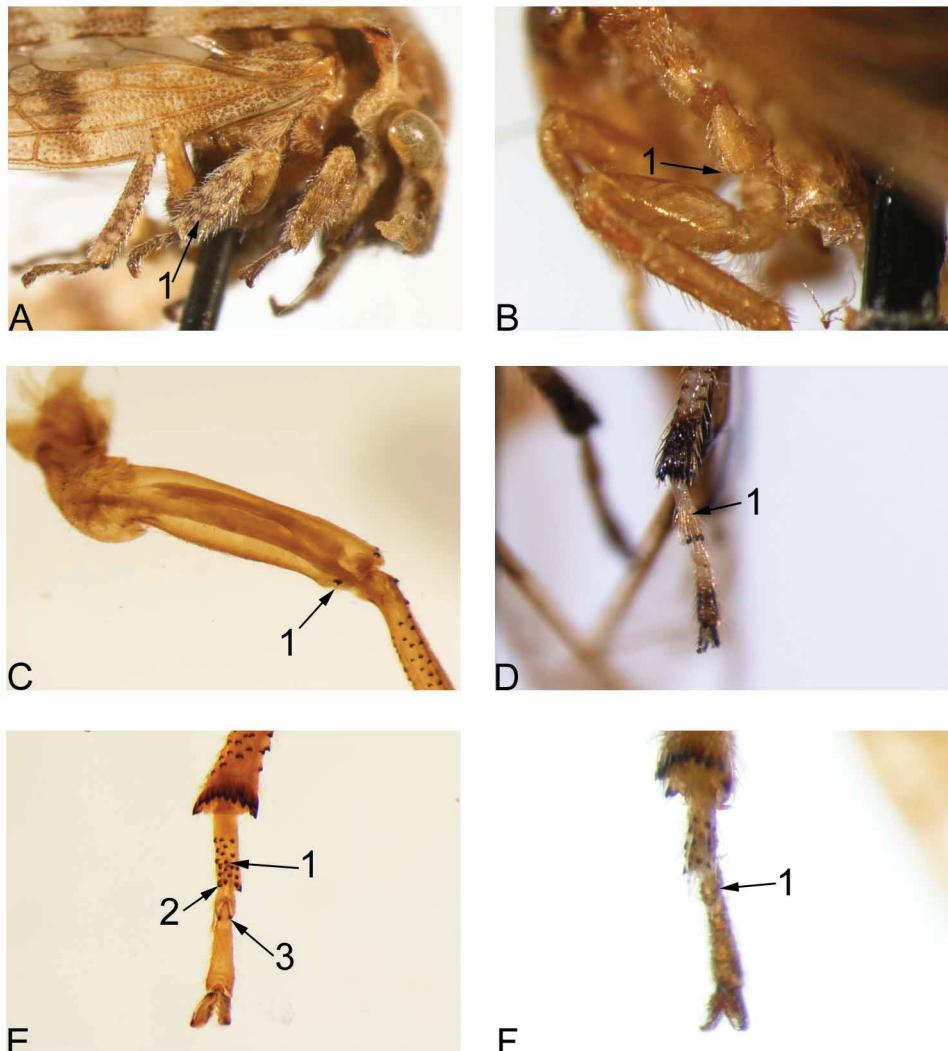
FIGURE 8. Selected right hind wings and characters states in the analysis. A, *Cyrtolobus vau* (Say): 1, veins R_{4+5} and M_{1+2} confluent for a great distance (r-m absent). B, *Helonica excelsa* (Fairmaire), #72-9b♂: 1, veins R_{4+5} and M_{1+2} free (r-m present).

The clade including *Grandolobus* as its basal lineage is supported by three changes, including a male style clasp that is gently rounded with a large tooth that is not strongly recurved (Fig. 10E, 1). The terminal clade containing *C. dixianus* and *Ophiderma* spp. is characterized by a male style clasp in lateral aspect with an additional tooth (Fig. 11A, 1) (with two reversals) and by the absence of paired posterior impressions with a separating ridge on the pronotum (one reversal) (Fig. 3F, 1). The grouping of *C. dixianus*, *C. inermis*, and *Atymna helena* was also recovered by Cast (2002).
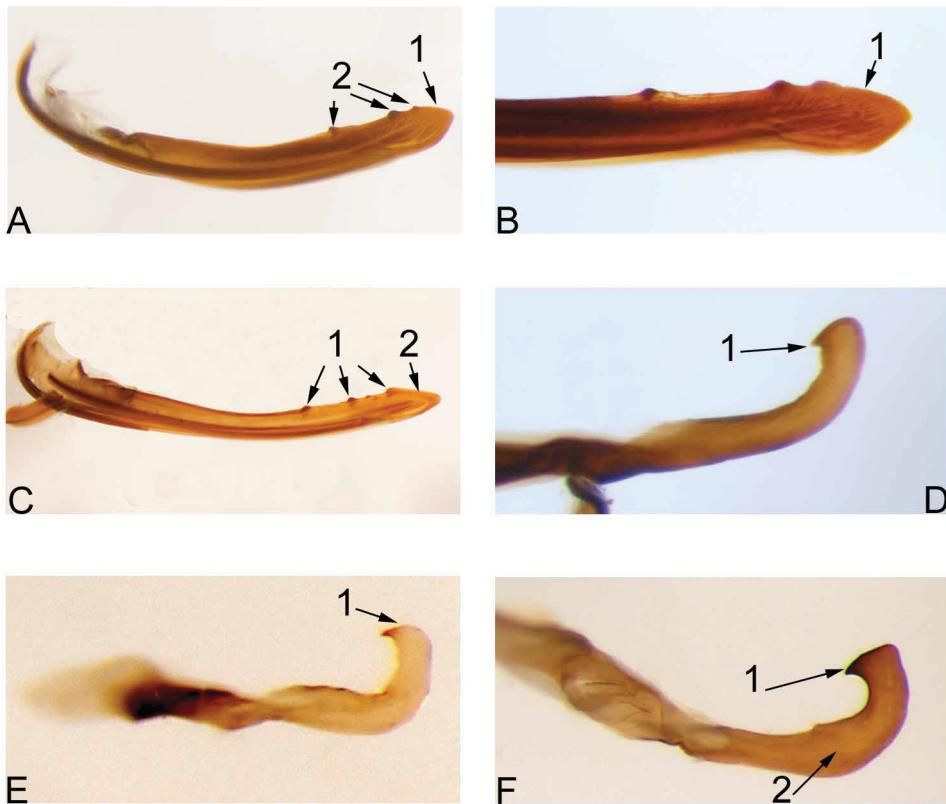
Prominent non-monophyletic genera within Smiliini *s.* Wallace in the analysis include *Atymna*, *Cyrtolobus* and *Xantholobus* (Fig. 1). This is not surprising considering the long history of moving species back and forth among these genera (Woodruff 1924; Metcalf and Wade 1965) and the plasticity of the characters used to distinguish them. For example, the central pronotal inflations that define *Xantholobus* in keys (Kopp and Yonke 1973c) are not evident in *X. intermedius* or the type species *X. inflatus*. Likewise, *Atymna* and *Cyrtolobus* are often distinguished in the same keys by the highest point of the pronotum—either behind (*Cyrtolobus*) or above the humeral notch

(*Atymna*). Although the type species of *Atymna*, *A. castaneae*, demonstrates a more anterior pronotal peak (Fig. 3B, 2), other species examined (e.g. *A. querci* and *A. helena*) have a more posterior pronotal peak (Fig. 3C, 1). Cast's (2001) analysis of the Smiliini *s.s.* also resulted in numerous paraphyletic genera. It is likely that future taxonomic work on this tribe will result in new combinations and possibly synonymies of genera. The apparent non-monophyly of these groups supports the need for an extensive generic revision of the Smiliini *s.* Wallace, preferably including nymphs and the examination of the primary types.

FIGURE 9. Selected taxa in lateral aspects, metathoracic legs, and characters states in the analysis. A, *Telamonanthe pulchella* (Ball), #09-184b♀: 1, legs short and flattened. B, *Cyrtolobus fuliginosus* (Emmons), #09-172b♀: 1, mesothoracic coxal process acute. C, *Archasia belfragei* Stål, left metathoracic leg, #09-160a♀: 1, femur ventral ablateral cucullate seta. D, *Smilirhexia naranja* McKamey, left metathoracic leg, holotype, ♂: 1, tarsomere I plantar cucullate setae absent. E, *A. belfragei*, left metathoracic leg, #09-160a♀: 1, tarsomere I plantar setae present; 2, tarsomere I apex with 3–4 cucullate setae; 3, tarsomere II apical cucullate setae present. F, *T. pulchella*, right metathoracic leg, #09-184b♀: 1, tarsomere II apical cucullate setae absent.

Nevertheless, the genus *Ophiderma* is monophyletic in the analysis, having relatively high Bremer support (>3) and 3 apomorphies. In this genus, the pronotum is convex dorsally (without a carina), and when viewed laterally, is flattened (Figs. 3D, 1; 3F, 1). Taxa within *Xantholobus inflatus* + *Ophiderma* all possess erect and obvious pronotal pubescence (Fig. 3D, 2). In Cast's (2002) phylogeny of the Smiliini *s.s.*, this genus is polyphyletic, with southwestern species (not coded here) basal to eastern species. Although not tested in the analysis, the genus *Smilia* is undoubtedly monophyletic based on the absence of forewing crossvein m-cu$_1$ (Fig. 7C, 1), and the clustering of *S. camelus* and *S. fasciata* in Cast's (2002) analysis.
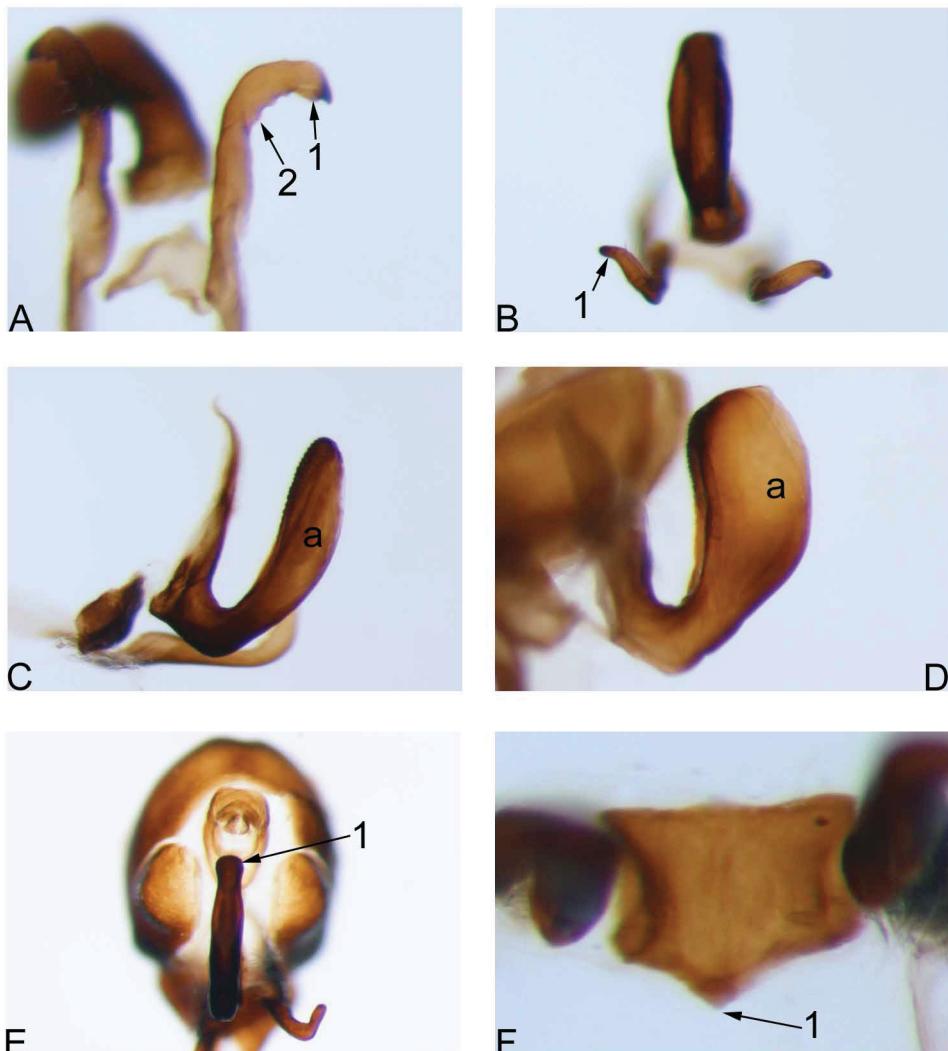
FIGURE 10. Selected female second valvulae (A–C) and male styles (D–F) in lateral aspect, and character states in the analysis. A, *Smilia camelus* (Fabricius), #09-160e♀: 1, second valvulae apex with dorsal and ventral margin converging distally, rounded; 2, second valvulae with middle and apical large teeth distinctly closer. B, *Cyrtolobus vau* (Say), #09-174d♀: 1, second valvulae distal small teeth. C, *Archasia belfragei* Stål, #09-160a♀: 1, second valvulae with 3 large teeth distally; 2, second valvulae apex with dorsal and ventral margin converging proximally, acuminate. D, *Xantholobus muticus* (Fabricius), #09-171e♂: 1, style clasp rounded with small recurved tooth. E, *Cyrtolobus fuliginosus* (Emmons), #09-172a♂: 1, style clasp slightly rounded with large tooth, not strongly recurved. F, *A. belfragei,* #09-160c♂: 1, style clasp angular with large recurved tooth; 2, style shank with pre-apical broadening.

Telamonini Goding 1892 *s.* Wallace, synonym reinstated

Diagnostic characters. Females almost always greater than 8 mm in length. Head dorsal margin with abrupt rise near eyes (Fig. 6C, 1); ocelli usually closer to eyes than each other (Fig. 6C, 2). Pronotum highly elevated and foliaceous in *Archasia* (Fig. 4A); with distinct median anterior horn or projection (Fig. 4E, 1) (absent in *Archasia* and *Carynota*); median carina present (Fig. 4F), complete or incomplete (Fig. 4F, 2); longitudinal rugae almost always present (Fig. 5A, 1); humeral angles enlarged (Fig. 6A, 1). Forewing partially concealed by pronotal posterior process (Fig. 4A); R, M, and Cu veins separate near base; veins crowded anteriorly and without large cells separating them (Fig. 7B); R_{4+5} vein confluent with M_{1+2} vein distad of M fork (Fig. 7B, 1). Hind wing with R_{4+5} and M_{1+2} veins free (or if fused, for short distance) (Fig. 8B, 1). Metathoracic tarsomere II apical cucullate setae usually present (Fig. 9E, 3); tibia with cucullate setal row I irregular or double. Dorsal and ventral margins of second valvulae apex converging proximally, apex acuminate (Fig. 10C, 2). Male style clasp usually angular, with large, recurved tooth (Fig. 10F, 1) (except in *Telamonanthe*); aedeagus width from lateral aspect variable but never narrow.
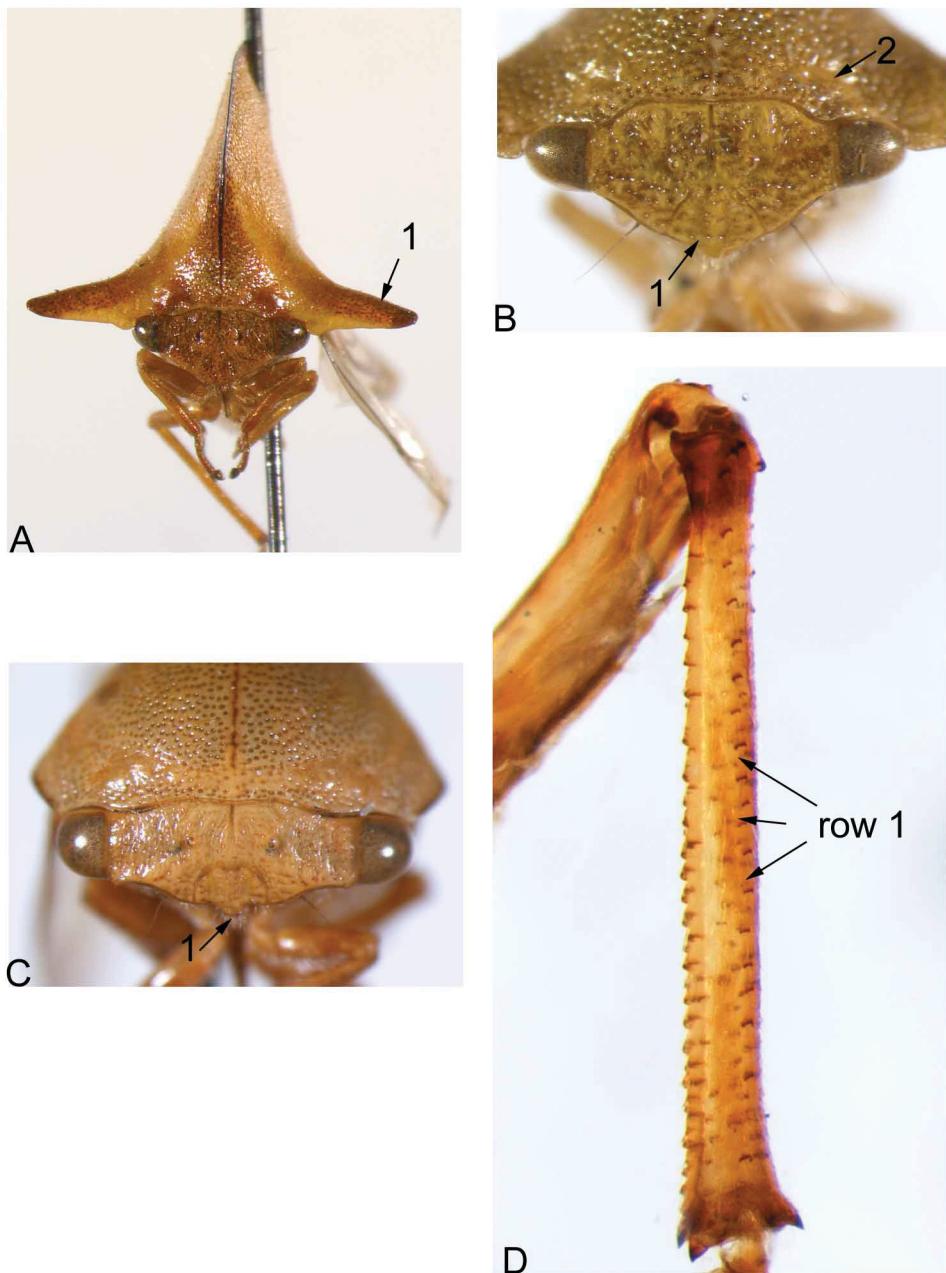
A large assemblage of genera form the monophyletic tribe Telamonini *s.* Wallace (Fig. 1, Table 2), herein reinstated from synonymy with Smiliini *s.l.* (Deitz 1975). This restructuring of the Smiliini *s.l.* is based upon the large number of morphological characters from the head, thorax, and abdomen that distinguish Telamonini *s.* Wallace from Smiliini *s.* Wallace (see key, diagnoses, and discussion below) and the relatively high character support (node 172: Bremer support 2, 5 character changes) in the phylogenetic analysis (Fig. 1, Table 6). Cast (2002) also recommended the reinstatement of Telamonini after recovering a monophyletic group of genera, sister group to Smiliini

s.s., in a phylogenetic analysis using mitochondrial DNA. The only difference between Telamonini *s.* Wallace and Telamonini *s.l.* Table 1 is the exclusion of *Hemicardiacus* and *Tropidarnis* as a result of this analysis, which along with the genus *Antianthe*, are basal to the Telamonini *s.* Wallace (Fig. 1). Including these genera, however, in Telamonini *s.* Wallace would result in a weaker morphological concept of the tribe, with unreliable, homoplastic synapomorphies defining the group. See below for a more detailed discussion of *Antianthe*, *Hemicardiacus*, and *Tropidarnis.*

FIGURE 11. Selected male styles, aedeagi, and connectives, and character states in the analysis. A, *Ophiderma flavicephala* Goding, style in ventral aspect, #09-171c♂: 1, style clasp with additional tooth; 2, style shank margin with additional small teeth. B, *O. flavicephala*, styles and aedeagus in posterior aspect, #09-171c♂: 1, style clasp shape visible from posterior aspect, angled laterally, and broadened dorsally. C, *Smilia camelus* (Fabricius), aedeagus from lateral aspect, #09-160g♂. D, *Archasia belfragei* Stål, aedeagus from lateral aspect, #09-160c♂. E, *Xantholobus muticus* (Fabricius), male genitalia from posterior aspect, #09-171e♂: 1, aedeagus with distinct dorsal head. F, *X. muticus*, #09-171e♂: 1, male connective with medial projection on anterior edge (in ventral aspect). a, aedeagus.
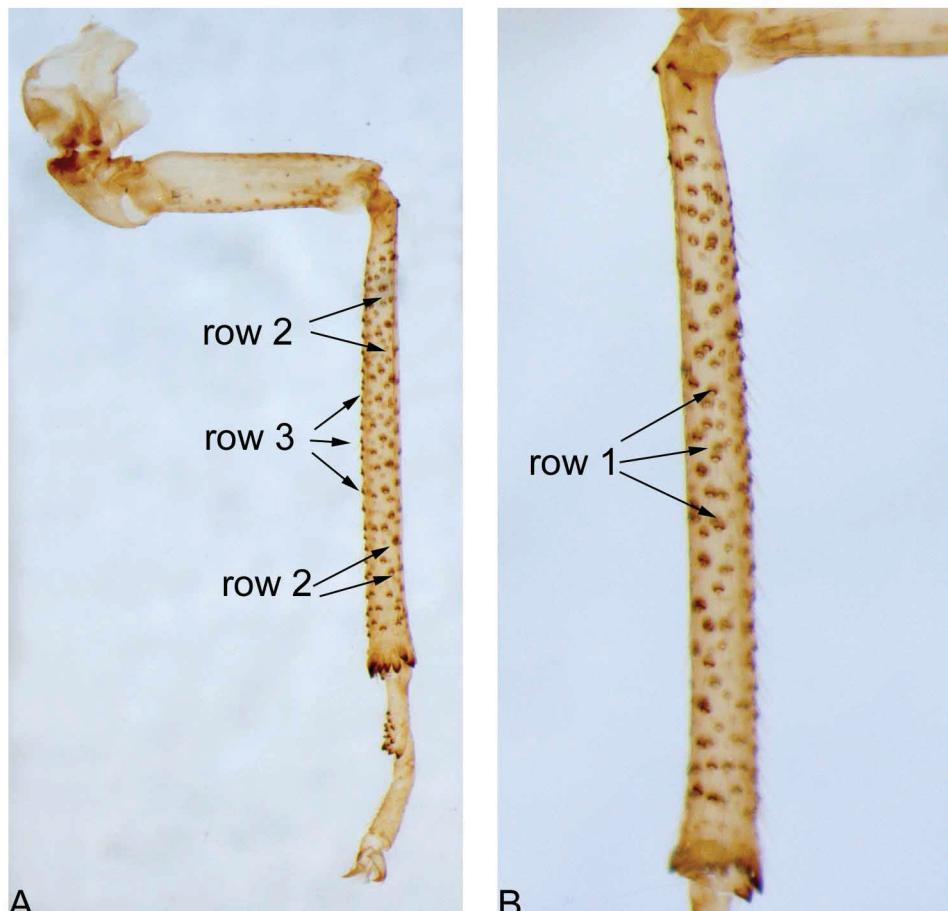
All Telamonini examined have forewing vein R_{4+5} confluent with vein M distad of or at the beginning of the fork of M (Fig. 7B, 1). A pronotal constriction or horn (Figs. 4D, 1; 4E, 1) is shared by all telamonines with the exception of *Archasia* (Fig. 4A) and *Carynota* (Fig. 4B). Moreover, the ancestors of these taxa lost a distinct pronotal horn or projection and evolved a pronotum that was smoothly rounded (*Carynota*) or highly elevated and foliaceous (*Archasia*). Similar evolution can be seen in some southern forms of *Telamona extrema* (Fig. 5B) which have a shape similar to *Archasia*, almost entirely without a distinct constriction. Finally, nearly all Telamonini have distinct longitudinal rugae on the posterior pronotum (Fig. 5A, 1).

FIGURE 12. *Antianthe* group and *Tropidarnis* I: A, *Hemicardiacus saundersi* Plummer, head and pronotum from anterior aspect, holotype, #71-363d♂: 1, pronotal humeral angles long, narrowed, and with anterior margin contacting lateral margin of eye. B, *Antianthe expansa* (Germar), head from anterior aspect, #11-005a♀: 1, frontoclypeus ventral margin appearing carinate, without ventral projection; 2, pronotal lateral supraocular callosities complete. C, *Tropidarnis tectigera* Fowler, head from anterior aspect, #72-10f♀: 1, frontoclypeus ventral margin with rounded projection. D, *T. tectigera*, row 1 of right metathoracic leg, #72-10f♀.

Several important features that characterize most telamonines and distinguish them from Smiliini *s.* Wallace were not synapomorphies (see above key), including: the apical segment of the proboscis noticeably shorter than the penultimate segment (Fig. 6B, 1); the ocelli closer to each other than to the eyes (Fig. 6C, 2); the dorsal margin of the head with an abrupt rise near the eyes (Fig. 6C, 1); enlarged humeral angles (Fig. 6A, 1); the forewing veins crowded anteriorly (Fig. 7B); the hind wing veins R_{4+5} and M_{1+2} free (Fig. 8B); the female second valvulae without small teeth distally and with the larger teeth evenly spaced among themselves (Fig. 10C); the male style clasp angular with a large recurved tooth (Fig. 10F, 1); and large-sized females (> 8.01 mm). Although Deitz (1975) noticed that the free R_{4+5} and M_{1+2} veins in the hind wing was an inconsistent character in the specimens he studied

(especially *Telamonanthe*), this feature seemed consistent when examining the large variety of telamonine genera and species for this study. It is possible that the inconsistency is only found in a few taxa or a small range of specimens. Dennis (1952) also described most male telamonines having style clasps with a "recurved apical hook." Similar to the wing venation example, the genus *Telamonanthe* was the only telamonine taxon viewed without this distinctive male style clasp shape, further supporting its peculiar morphology and basal placement within the tribe.
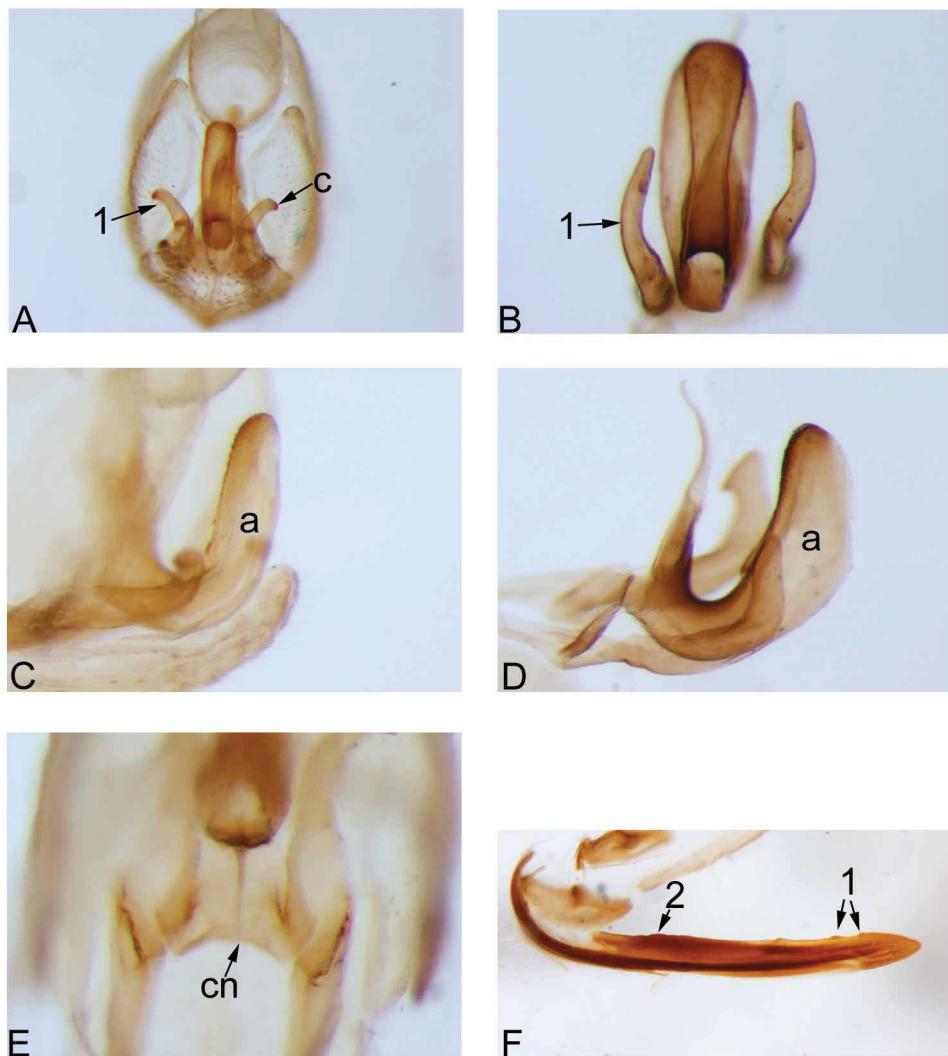
FIGURE 13. *Antianthe* group: A–B, *Antianthe expansa* (Germar), left metathoracic leg, #09-183a♂.

The analysis resulted in a basal Telamonini lineage including *Telamonanthe*, two lineages of single species, and one large clade divided into two major lineages (Fig. 1). The most basal clade includes *Telamonanthe* and two related species currently in *Heliria* and *Telamona*. This is among the more highly supported groups in the analysis (Bremer support >3, 5 character changes) (Fig. 1), distinguished by the heavy anterior sclerotization in the basal half of the forewing (Fig. 7D, 1), short and flat leg segments (Fig. 9A, 1), metathoracic tarsomere II without apical cucullate setae (Fig. 9F, 1), and medium-sized females (6.01–8 mm). *Telamonanthe* also formed the basal clade in Cast's (2002) Bayesian analysis of the Telamonini.

Most of the remaining telamonines are included in a large clade (sister group to *Heliria sinuata*) formed by two sister lineages (Fig. 1). This group is supported by the presence of a ventral ablateral cucullate seta on the metathoracic femur (Fig. 9C, 1), a unique synapomorphy. The first lineage within this large clade includes various *Glossonotus* spp., *Heliria* spp., *Telonaca*, *Thelia*, and an undescribed telamonine taxon. This group has low support (Bremer support=1, 2 character changes) in the analysis (Table 6) and is characterized by a median anterior horn or constriction that is laterally flattened apically and with a narrow rounded apex (except *H. cornutula*) (Figs. 4D, 1; 4F, 1). Species in *Glossonotus* + *Thelia* possess a distinct horn-like projection located anterior or above the humeral angles (Fig. 5D, 1). The nymphs of *Glossonotus acuminatus*, *Heliria scalaris*, and *Thelia bimaculata*, illustrated and examined by Quisenberry *et al.* (1978), all have at least one median dorsal spine on the thorax and abdomen, providing independent support for this clade. In Cast's (2002) Telamonini phylogeny, *Thelia bimaculata* formed a single basal lineage, sister group to five other clades within the tribe. The first of these clades was comprised of *G.*

crataegi and an *Archasia* sp., followed by a group with two species of *Glossonotus* (including *G. acuminatus*), three *Heliria* spp. and two *Telamona* spp.

FIGURE 14. *Antianthe* group and *Tropidarnis* II: A, *Antianthe expansa* (Germar), male style from posterior aspect, #09-183a♂: 1, style clasp from posterior aspect angled laterally. B, *Tropidarnis tectigera* Fowler, male style from posterior aspect, #72-10g♂: 1, style clasp from posterior aspect vertical. C, *A. expansa*, aedeagus from lateral aspect, #09-183a♂. D, *Tropidarnis tectigera*, aedeagus from lateral aspect, #72-10g♂. E, *A. expansa*, connective from dorsal aspect #09-183a♂. F, *A. expansa*, female second valvulae from lateral aspect, #09-183b♀: 1, second valvulae with middle and apical large teeth distinctly closer; 2, second valvulae basal teeth. a, aedeagus. c, style clasp. cn, connective.

The second lineage in this large group, also with low support (Bremer support=1, 2 character changes) (Fig. 1), includes *Archasia* spp., *Carynota*, *Helonica*, *Palonica*, and many *Telamona* spp. All taxa in this group have a smoothly textured pronotum without a deep posterior fovea (Fig. 4A), and a scalloped media carina on the median anterior projection (Fig. 5B, 1). Indeed, the nymphs of three genera examined by Quisenberry *et al.* (1978) within this clade, *Archasia pallida*, *Carynota mera*, *Telamona monticola*, are remarkably similar in anatomy, having reduced overall features and each lacking median dorsal spines on the thorax and abdomen. Within this group, the clade *Telamona unicolor* + *T. monticola* is well supported (Bremer support >3, 3 character changes,). These two species, along with some other *Telamona* spp. not included in the analysis, have an anteriorly inflated pronotum (Fig. 5C, 1). Taxa within the clade *Telamona decorata* + (*Carynota mera* + (*Archasia*)) all have distinct erect pronotal pubescence (Fig. 4C, 1). The genus *Archasia* was also monophyletic in this analysis supported by a highly elevated and foliaceous pronotum with a dark median carina extending the entire pronotal length (Fig. 4A, 1). *Archasia* nymphs also have a unique smoothly rounded pronotum, providing additional evidence to support the

validity of this genus (Quisenberry *et al.* 1978). Cast (2002) recovered a group of similar taxa in his molecular analysis, including *A. belfragei*, *Glossonotus univittatus*, *Helonica*, *T. decorata*, *T. extrema*, *T. monticola*, *T. unicolor*, and various other *Telamona* spp. Notable differences in this clade between Cast (2002) and the present analysis were the placement of *Carynota mera* (a basal lineage in Cast) and *Glossonotus univittatus* (placed with the *G. acuminatus*, *Heliria*, and *Telonaca* clade in the present phylogeny).

Based on the phylogenetic analysis and the characters discovered in this study, the two largest Telamonini *s.* Wallace genera, *Telamona* and *Heliria*, are not monophyletic. Morphological variation within these taxa clearly merits a rigorous taxonomic revision, likely resulting in new combinations and/or new genera. Ball (1931) defined the genus *Telamona* as treehoppers having a distinct, rather quadrangular crest with a variably shaped dorsal margin and *Heliria* as treehoppers having a quadrangular crest with a step-like dorsal margin. Although consistent in some cases (Ball 1931), these pronotal characters themselves cannot be used to separate *Heliria* and *Telamona* from each other or other telamonines. In many situations, the shape of the pronotum is a subjective and arbitrary characterization, and a matter of one's perspective. For example the pronotal crest in certain *Heliria* species (*H. clitella*, *H. fitchi*, *H. sinuata*), *Helonica*, and *Telamonanthe*, is very similar to the crest described by Ball (1931) that defines *Telamona*. Furthermore, the shape of the pronotal crest has been shown to vary within species and sometimes populations, as seen in *Heliria praealta* (photographed on the same branch!) (Yothers and Allen 1941). More than one form of *Telamona* nymph has also been described (Quisenberry *et al.* 1978). Nevertheless, the analysis presented here shows that some aspects of the pronotal shape are useful in grouping taxa (dorsal margin scalloped vs. wavy). Like many other morphological features in insects, structures that vary in some taxa may be relatively constant in others. Wood and Pesek (1992) argued for the importance of the pronotum in classifications, although it is difficult to translate these shape character states for cladistic analyses.

Antianthe, *Hemicardiacus*, and *Tropidarnis*, Smiliinae, *incertae sedis*

The tribal status of *Antianthe*, *Hemicardiacus*, and *Tropidarnis* is uncertain based on the variable placement of *Antianthe* and *Tropidarnis* in the phylogenies of Cast (2002) and this work, and are herein placed Smiliinae, *incertae sedis*. In Cast's (2002) molecular phylogeny of the Smiliinae, *Antianthe* is nested within a clade of Polyglyptini genera (resulting in a paraphyletic Smiliini *s.l.*), a group sister to the Smiliini *s.l.* in his analysis, and *Tropidarnis* is nested in the Telamonini between the basal *Telamonanthe* and the remaining telamonine genera. Here (Fig. 1), *Antianthe* and *Hemicardiacus* form the basal monophyletic group of **clade 3**, sister to *Tropidarnis* + Telamonini, while *Tropidarnis* is the sister group to the Telamonini *s.* Wallace. These genera were not placed within Telamonini *s.* Wallace here because their inclusion would have resulted in a weaker concept of the tribe, defined by homoplastic synapomorphies. Nevertheless, these taxa share certain features with the Telamonini, such as an abrupt rise on the dorsal margin of the head near the eyes, enlarged humeral angles, and the forewing veins crowded anteriorly. Despite their doubtful tribal placement, in this analysis, both *Antianthe* and *Tropidarnis* form lineages with distinctive distributions, and morphological and biological traits. The only specimen examined of *Hemicardiacus* was the undissected male holotype, which resulted in missing data for more than 30 characters. The collection of additional specimens of this genus should help determine its tribal placement and relation to *Antianthe*. Future works with increased taxon sampling should help elucidate the relationships of these genera to other Smiliinae.

Antianthe and *Hemicardiacus* (*Antianthe* group) are distinguished from the Smiliini *s.* Wallace, Telamonini *s.* Wallace, and *Tropidarnis* by the following features: frontoclypeal inferior margin without a ventral projection (Fig. 12B, 1); pronotum highly elevated and foliaceous (Fig. 12A); and pronotal humeral angles enlarged, long, and often narrowed with the anterior margin contacting the lateral margin of eye (Fig. 12A, 1). The placement of *Antianthe* near various Polyglyptini genera in Cast's (2002) phylogeny of the Smiliinae deserves further scrutiny considering the differences between these taxa in the characteristics of the female second valvulae (the second valvulae of *Antianthe* is very similar to the second valvulae of genera in Smiliini *s.* Wallace and Telamonini *s.* Wallace), the absence of pronotal longitudinal rugae in *Antianthe* (present in most Polyglyptini), and the enlarged humeral angles in *Antianthe* (absent in Polyglyptini), among other features.

Both *Antianthe* and *Hemicardiacus* have a primarily Neotropical distribution, apparently localized in high altitudes (Table 2) (Plummer 1945; McKamey 1998; Cast 2002). *Antianthe* is the only genus, when compared with the Smiliini *s.* Wallace and Telamonini *s.* Wallace, known from the plant families Lauraceae, Rubiaceae, and Solan-

aceae (Ballou 1935), while *Hemicardiacus* is reported from oak (*Quercus*) (Plummer 1945). Further, *Antianthe* is the only taxon from these groups to show subsocial (maternal egg guarding, ant-attended nymphal aggregations) and multivoltine behaviors (Wood 1984; Cast 2002). Most Smiliini and Telamonini are solitary as adults and nymphs, univoltine, and monophagous (Wood 1984; Cast 2002), but *Atymna castaneae*, *Cyrtolobus vau*, *Ophiderma pubescens*, *Telamona ampelopsidis*, *T. unicolor*, and *Thelia bimaculata* are listed as being attended by ants (Funkhouser 1917).

TABLE 4. Data Matrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Antianthe expansa	1	2	2	2	1	1	1	1	1	2	1	2	2	2	2	2	1	?	?	?
Antianthe foliacea	1	2	2	2	1	1	1	1	1	2	1	2	2	2	2	2	1	?	?	?
Archasia auriculata	2	2	1	2	1	1	1	1	1	2	1	2	2	2	2	2	1	?	?	?
Archasia belfragei	2	2	1	2	2	1	1	1	1	2	1	2	2	2	2	2	1	?	?	?
Archasia pallida	2	2	1	2	2	1	1	1	1	2	1	2	2	2	2	2	1	?	?	?
Ashmeadea carinata	2	1	2	1	1	1	2	2	2	2	1	1	1	2	1	2	1	?	?	?
Atymna castaneae	2	1	2	1	1	1	1	1	1	2	1	1	2	2	1	2	1	?	?	?
Atymna distincta	2	1	2	1	1	1	2	2	2	2	1	1	1	2	1	2	1	?	?	?
Atymna helena	2	1	2	1	1	1	1	2	1	2	1	1&2	2	2	1	2	1	?	?	?
Bryantopsis ensigera	1	1	2	1	1	1	1	1	1	2	1	1	2	2	1	2	2	1	2	1
Carynota mera	2	2	1	2	2	1	1	2	1	1	?	?	?	2	1	2	1	?	?	?
Cyrtolobus arcuatus	2	1	2	1	1	1	2	2	2	2	1	1	1	2	1	2	1	?	?	?
Cyrtolobus dixianus	2	1	2	1	1	1	2	2	2	2	1	1	2	2	1	2	1	?	?	?
Cyrtolobus fenestratus	2	1	2	1	1	1	2	2	2	2	1	1	1	2	1	2	1	?	?	?
Cyrtolobus inermis	2	1	2	1	1	1	1	2	1	2	1	1	2	2	1	2	1	?	?	?
Cyrtolobus tuberosus	2	1	2	1	1	1	2	2	2	2	1	1	1	2	1	2	1	?	?	?
Cyrtolobus vanduzii	2	1	?	?	1	1	2	2	2	2	1	1	1	2	1	2	1	?	?	?
Cyrtolobus vau	2	1	2	1	1	2	2	2	2	2	1	1	2	2	1	2	1	?	?	?
Glossonotus acuminatus	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	2	2	1
Glossonotus univittatus	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	1	1	1
Godingia guerreroensis	2	1	2	1	1	1	2	2	1	2	1	1	1	2	1	2	1	?	?	?
Grandolobus grandis	2	1	2	1	1	1	2	2	2	2	1	1	1	2	1	2	1	?	?	?
Heliria cornutula	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	2	2	2
Heliria cristata	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	2	2	1
Heliria mexicana	2	1	2	2	1	1	1	1	1	2	1	1	2	2	1	2	2	2	2	2
Heliria praealta	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	1	2	1
Heliria scalaris	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	1	2	2
Heliria sinuata	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	2	2	2
Helonica excelsa	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	2	2	1
Hemicardiacus saundersi	1	1	1	2	1	1	1	1	1	2	1	2	2	2	2	2	1	?	?	?
Heranice miltoglypta	2	1	2	2	1	1	1	1	1	2	1	1	2	2	1	2	1	?	?	?
Idioderma virescens	2	1	?	?	1	1	1	1	1	1	?	?	?	2	1	1	1	?	?	?
Ophiderma pubescens	2	1	2	1	1	2	1	2	1	1	?	?	?	2	1	1	1	?	?	?
Ophiderma salamandra	2	1	2	1	1	2	1	2	1	1	?	?	?	2	1	1	1	?	?	?
Palonica nogalana	2	2	1	2	1	1	1	1	1	2	2	1	2	2	1	2	2	2	2	1
Palonica pyramidata	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	2	2	1

TABLE 4. (continued)

										1	1	1	1	1	1	1	1	1	1	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Palonica tremulata	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	2	2	1
Quadrinarea perezi	2	2	3	1	1	1	1	2	1	1	?	?	?	2	1	1	1	?	?	?
Smilia fasciata	2	1	2	1	1	1	2	1	2	2	1	1	1	2	2	2	1	?	?	?
Smilirhexia naranja	1	1	1	1	1	1	1	1	1	1	?	?	?	1	1	2	1	?	?	?
Telamona ampelopsidis	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	2	2	1
Telamona balli	2	1	2	2	1	1	1	1	1	2	1	1	2	2	1	2	2	2	2	2
Telamona collina	2	2	1	2	3	1	1	1	1	2	2	1	2	2	1	2	2	2	2	1
Telamona decorata	2	2	1	2	3	1	1	1	1	2	2	1	2	2	1	2	2	2	2	1
Telamona extrema	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	1	1	1
Telamona gibbera	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	1	2	1
Telamona monticola	2	2	1	2	3	1	1	1	1	2	2	1	2	2	1	2	2	1	1	1
Telamona salvini	2	2	1	2	1	1	1	1	1	2	1	1	2	2	1	2	2	2	2	2
Telamona unicolor	2	2	1	2	3	1	1	1	1	2	2	1	2	2	1	2	2	1	1	1
Telamonanthe rileyi	2	1	2	2	1	1	1	1	1	2	1	1	2	2	1	2	2	1&2	2	2
Telonaca alta	2	1	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	2	2	1
Thelia bimaculata	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	1	2	1
Thuris fenestratus	1	1	3	1	1	2	?	1	2	2	1	1	2	2	1	2	1	?	?	?
Tropidarnis tectigera	2	1	2	2	1	1	1	1	1	2	1	1	2	2	1	2	1	?	?	?
Xantholobus inflatus	2	1	2	1	1	1	2	2	1	1	?	?	?	2	1	2	1	?	?	?
Xantholobus muticus	2	1	2	1	1	1	2	2	2	2	1	1	1	2	1	2	1	?	?	?
Xantholobus tumidus	2	1	2	1	1	1	1	1	2	2	1	1	1	2	1	2	1	?	?	?
Ceresa vitulus	2	1	2	1	1	1	1	1	1	2	?	1	2	1	1	2	1	?	?	?
Smiliini sp. 1	2	1	1	1	1	1	2	1	1	2	1	1	1	2	2	2	1	?	?	?
Smiliini sp. 2	2	1	2	1	1	1	1	2	2	2	2	1	2	2	1	2	1	?	?	?
Spissistilus festinus	2	1	2	1	1	1	1	1	1	2	?	1	2	1	1	2	1	?	?	?
Telamonini sp.	2	2	1	2	2	1	1	1	1	2	2	1	2	2	1	2	2	2	1	1

continued

	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Antianthe expansa	?	?	?	?	?	?	?	2	1	1	?	2	3	1	1&2	1	2	2	2	1
Antianthe foliacea	?	?	?	?	?	?	?	2	1	1	?	2	3	1	1	1	2	2	2	1
Archasia auriculata	?	?	?	?	?	?	?	2	1	1	?	2	1	2	2	1	2	1	2	1
Archasia belfragei	?	?	?	?	?	?	?	2	1	1	?	2	1	2	2	1	2	1	2	1
Archasia pallida	?	?	?	?	?	?	?	2	1	2	1	2	1	2	2	1	2	1	2	1
Ashmeadea carinata	?	?	?	?	?	?	?	2	1	1	?	1	?	1	2	1	2	2	2	1
Atymna castaneae	?	?	?	?	?	?	?	2	1	1	?	1	?	1	2	1	2	2	2	1
Atymna distincta	?	?	?	?	?	?	?	2	1	1	?	1	?	1	1	1	2	2	2	1
Atymna helena	?	?	?	?	?	?	?	3	1	1	?	1	?	1	1&2	1	2	2	2	1
Bryantopsis ensigera	1	2	?	?	?	1	1	1	1	2	2	1	?	1	2	2	2	1	1	1
Carynota mera	?	?	?	?	?	?	?	2	1	2	1	2	1	2	2	1	2	1	2	1
Cyrtolobus arcuatus	?	?	?	?	?	?	?	2	1	1	?	1	?	1	2	1	2	2	2	1

TABLE 4. (continued)

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Cyrtolobus vanduzii	?	?	?	?	?	?	?	2	1	1	?	1	?	1	2	1	2	2	2	1
Cyrtolobus vau	?	?	?	?	?	?	?	2	1	1	?	1	?	1	2	1	2	2	2	1
Glossonotus acuminatus	1	2	?	?	?	2	1	1	1	2	1	2	2	1	2	1	2	1	2	1
Glossonotus univittatus	1	1	?	?	?	2	1	1	1	2	1	2	1	2	2	1	2	1	2	1
Godingia guerreroensis	?	?	?	?	?	?	?	3	1	1	?	1	?	1	2	1	2	2	2	1
Grandolobus grandis	?	?	?	?	?	?	?	2	1	1	?	1	?	1	1	1	2	2	2	1
Heliria cornutula	2	?	1	1	3	1	1	2	1	2	1	2	2	1	2	1	2	1	2	1
Heliria cristata	2	?	1	1	3	2	1	2	1	2	1	2	2	1	2	1	2	1	2	1
Heliria mexicana	2	?	1	1	1	1	2	2	1	2	1	2	2	1	2	2	2	1	2	1
Heliria praealta	2	?	2	1	3	1&2	1	2	1	2	1	2	2	1	2	1	2	1	2	1
Heliria scalaris	2	?	1	1	3	2	1	2	1	2	1	2	2	1	2	1	2	1	2	1
Heliria sinuata	2	?	1	1	3	1	2	2	1	2	1	2	2	1	2	1	2	1	2	1
Helonica excelsa	2	?	1	1	2	1	1	2	1	2	1	2	2	1	2	1	2	1	2	1
Hemicardiacus saundersi	?	?	?	?	?	?	?	2	1	1	?	2	3	1	2	1	2	1	2	1
Heranice miltoglypta	?	?	?	?	?	?	?	2	1	2	2	2	1	1	2	2	2	1	2	1
Idioderma virescens	?	?	?	?	?	?	?	2	1	1	?	1	?	1	1	1	2	2	1	3
Ophiderma pubescens	?	?	?	?	?	?	?	2	1	1	?	1	?	2	2	1	2	2	2	1
Ophiderma salamandra	?	?	?	?	?	?	?	2	1	1	?	1	?	2	2	1	2	2	2	1
Palonica nogalana	2	?	1	2	2	1	2	2	1	2	1	2	2	1	2	1	2	1	2	1
Palonica pyramidata	2	?	1&2	1&2	2&3	1&2	2	2	1	2	1	2	2	1	2	1	2	1	2	1
Palonica tremulata	2	?	1	2	2	1	2	2	1	2	1	2	2	1	2	1	2	1	2	1
Quadrinarea perezi	?	?	?	?	?	?	?	1	1	1	?	1	?	1&2	2	1	2	2	1	2
Smilia fasciata	?	?	?	?	?	?	?	2	1	1	?	1	?	1	2	1	2	2	2	1
Smilirhexia naranja	?	?	?	?	?	?	?	3	1	1	?	1	?	1	1	1	1	2	2	1
Telamona ampelopsidis	2	?	1	1	2	1	1	2	1	2	1	2	2	1	2	1	2	1	2	1
Telamona balli	2	?	?	1	1	1	2	2	1	2	1	2	2	1	2	2	2	1	2	1
Telamona collina	2	?	1	1	2	1	1	2	1	2	1	2	2	1	2	1	2	1	2	1
Telamona decorata	2	?	1	1	2	1	2	2	1	2	1	2	1	2	2	1	2	1	2	1
Telamona extrema	2	?	1	1	2	1	2	2	1	1	?	2	1	1	2	1	2	1	2	1
Telamona gibbera	2	?	1	1	2	1	2	2	1	2	1	2	1	1	2	1	2	1	2	1
Telamona monticola	2	?	1	1	2	1	2	2	1	2	1	2	1	1	2	1	2	1	2	1
Telamona salvini	2	?	1	1	1	1	2	2	1	2	1	2	2	1	2	1	2	1	2	1
Telamona unicolor	2	?	1	1	2	1	2	2	1	2	1	2	1&2	1	2	1	2	1	2	1
Telamonanthe rileyi	2	?	1	1	1	1	2	2	1	2	1	2	2	1	2	2	2	1	2	1
Telonaca alta	2	?	2	1	3	2	1	2	1	2	1	2	2	1	2	1	2	1	2	1
Thelia bimaculata	1	2	?	?	?	2	1	1	1	2	1	2	1	1	2	1	2	1	2	1
Thuris fenestratus	?	?	?	?	?	?	?	2	1	1	?	1	?	1	1	1	2	2	1	2
Tropidarnis tectigera	?	?	?	?	?	?	?	2	1	1	?	2	1	1	1	1	2	1	2	1
Xantholobus inflatus	?	?	?	?	?	?	?	2&3	2	1	?	1	?	2	2	1	2	2	2	1
Xantholobus muticus	?	?	?	?	?	?	?	3	1	1	?	1	?	1	2	1	2	2	2	1
Xantholobus tumidus	?	?	?	?	?	?	?	3	1	1	?	1	?	1	2	1	2	2	2	1
Ceresa vitulus	?	?	?	?	?	?	?	3	1	1	?	1	?	1	1	1	1	2	2	2

	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Smiliini sp. 1	?	?	?	?	?	?	?	2	1	1	?	2	2	1	2	1	2	2	2	1
Smiliini sp. 2	?	?	?	?	?	?	?	3	1	1	?	1	?	1	2	1	2	2	2	1
Spissistilus festinus	?	?	?	?	?	?	?	3	1	1	?	1	?	1	1	1	1	2	2	2
Telamonini sp.	2	?	2	1	2	2	1	1	1	2	1	2	2	1	2	1	2	1	2	1

continued.

	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Antianthe expansa	3	1	2	2	1	1	?	2	1	2	2	1	2	2	2	2	1	2	1	2
Antianthe foliacea	3	1	2	2	1	1	?	2	1	2	2	1	2	2	2	2	1	2	1	2
Archasia auriculata	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	2
Archasia belfragei	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	2
Archasia pallida	2	1	1	?	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	1
Ashmeadea carinata	3	1	2	2	1	1	?	2	1	2	2	1	1	2	2	1	1	2	1	1
Atymna castaneae	3	1	2	2	1	2	1	2	1	2	2	1	1	2	2	2	1	2	1	1
Atymna distincta	3	1	2	?	1	2	1	2	1	2	2	1	1	2	2	2	1	2	1	1
Atymna helena	3	1	2	2	1	2	1	2	1	2	2	1	1	2	2	2	1	2	1	1
Bryantopsis ensigera	3	?	2	?	1	1	?	2	1	2	2	1	1	2	2	1	?	1	2	1
Carynota mera	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	2
Cyrtolobus arcuatus	3	1	2	?	1	2	1	2	1	2	2	1	1	2	2	2	1	2	1	1
Cyrtolobus dixianus	3	1	2	?	1	2	1	2	1	2	2	1	1	2	2	2	1	2	1	1
Cyrtolobus fenestratus	3	1	2	2	1	2	1	2	1	2	2	1	1	2	2	2	1	2	1	1
Cyrtolobus inermis	3	1	2	2	1	2	1	2	1	2	2	1	1	2	2	2	1	2	1	1
Cyrtolobus tuberosus	3	1	2	2	1	2	1	2	1	2	2	1	1	2	2	2	1	2	1	1
Cyrtolobus vanduzii	3	2	2	?	1	2	1	2	1	1	2	1	1	2	2	2	1	2	1	1
Cyrtolobus vau	3	1	2	2	1	2	1	2	1	2	2	1	1	2	2	2	1	2	1	1
Glossonotus acuminatus	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	2
Glossonotus univittatus	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	2
Godingia guerreroensis	3	1	2	?	1	2	1	2	1	2	2	2	1	2	2	2	1	2	1	?
Grandolobus grandis	3	1	2	2	1	2	1	2	1	2	2	1	1	2	2	2	1	2	1	1
Heliria cornutula	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	2	2	1	2
Heliria cristata	2	1	1	1&2	1	2	2	2	2	2	2	1	2	2	2	2	2	2	1	2
Heliria mexicana	2	1	1	?	2	1	?	2	1	2	2	1	1	2	2	2	?	2	1	2
Heliria praealta	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	2
Heliria scalaris	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	2	2	1	2
Heliria sinuata	2	1	1	?	1	2	2	2	1	2	2	1	2	2	2	2	1	2	1	2
Helonica excelsa	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	1
Hemicardiacus saundersi	2	1	1	2	1	1	?	2	1	2	2	1	?	2	2	2	?	?	?	?
Heranice miltoglypta	3	1	2	2	1	1	?	2	1	2	2	1	1	2	2	2	1	1	2	1
Idioderma virescens	3	1	2	2	1	2	2	2	1	2	2	1	1	1	2	2	1	2	1	?
Ophiderma pubescens	3	1	2	2	1	2	1	2	1	2	2	2	1	2	2	2	1	2	1	2
Ophiderma salamandra	3	1	2	2	1	2	1	2	1	2	2	2	1	2	2	2	1	2	1	1
Palonica nogalana	2	1	1	?	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	1

TABLE 4. (continued)

	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Palonica pyramidata	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	2
Palonica tremulata	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	1
Quadrinarea perezi	3	1	2	2	1	1	?	1	1	2	2	1	1	1	1	1	1	1	1	1
Smilia fasciata	3	2	2	2	1	2	1	2	1	2	2	1	1	2	2	2	1	2	1	1
Smilirhexia naranja	2	1	1	1	1	1	?	2	1	1	2	1	2	2	2	1	1	?	?	?
Telamona ampelopsidis	2	1	1	?	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	1
Telamona balli	2	1	1	?	2	1	?	2	1	2	2	1	1	2	2	2	?	2	1	2
Telamona collina	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	1
Telamona decorata	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	2
Telamona extrema	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	2
Telamona gibbera	2	1	1	?	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	1
Telamona monticola	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	1
Telamona salvini	2	1	1	?	1	2	2	2	1	2	2	1	2	2	2	2	1	2	1	2
Telamona unicolor	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	1
Telamonanthe rileyi	2	1	1	2	2	1	?	2	1	2	2	1	1	2	2	2	1	2	1	2
Telonaca alta	2	1	1	2	1	2	2	2	2	2	2	2	2	2	2	2	1	2	1	2
Thelia bimaculata	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	1	2	1	2
Thuris fenestratus	2	1	2	2	1	1	?	2	1	2	1	1	1	1	2	2	?	1	1	1
Tropidarnis tectigera	3	1	1	2	1	1	?	2	1	2	2	1	1&2	1	2	2	1	2	1	1
Xantholobus inflatus	2&3	1	2	2	1	1	?	2	1	2	2	2	1	2	2	2	1	2	1	1
Xantholobus muticus	3	1	2	2	1	2	1	2	1	2	2	2	1	2	2	2	1	2	1	1
Xantholobus tumidus	3	1	2	2	1	2	1	2	1	2	2	2	1	2	2	2	1	2	1	1
Ceresa vitulus	3	1	2	1	1	1	?	2	1	2	3	1	2	1	2	1	1	2	1	1
Smiliini sp. 1	3	1	1	?	1	2	2	2	1	2	2	2	1	2	2	2	2	?	?	?
Smiliini sp. 2	3	1	2	?	1	1	?	2	1	2	2	2	1	2	2	2	1	?	?	?
Spissistilus festinus	3	1	1	1	1	1	?	2	1	2	3	1	2	1	2	1	1	2	1	1
Telamonini sp.	2	1	1	2	1	2	2	2	2	2	2	1	2	2	2	2	2	2	1	2

continued.

	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
Antianthe expansa	2	1	2	2	2	2	1	2	1	1	3	1	1	1	1	1	3	1
Antianthe foliacea	1	1	2	2	2	1	1	2	1	1	3	1	1	1	1	1	3	1
Archasia auriculata	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Archasia belfragei	1	2	1	2	2	2	1	1	2	1	3	1	1	1	1	2	4	1
Archasia pallida	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Ashmeadea carinata	1	2	2	2	2	1	1	2	1	2	3	1	1	1	1	1	2	1
Atymna castaneae	1	2	2	2	2	1	1	2	1	2	3	1	1	1	2	1	2	1
Atymna distincta	1	2	2	2	2	1	1	2	1	2	3	1	1	1	2	1	3	1
Atymna helena	1	2	1	2	2	1	2	1	1	2	3	1	1	1	1	1	3	1
Bryantopsis ensigera	1	1	1	1	?	?	?	?	?	?	3	1	1	1	1	1	3	1
Carynota mera	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1

TABLE 4. (continued)

| | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 |
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
Cyrtolobus arcuatus	1	2	1	2	2	1	2	1	2	2	3	1	1	1	2	1	3	1
Cyrtolobus dixianus	1	2	2	2	2	1	1	2	1	2	3	1	1	1	1	1	3	1
Cyrtolobus fenestratus	1	2	1	2	2	1	2	2	1	2	3	1	1	1	2	1	3	1
Cyrtolobus inermis	1	2	2	2	2	1	2	2	1	2	3	1	1	1	1	1	3	1
Cyrtolobus tuberosus	2	2	2	2	2	1	1	2	1	2	3	1	1	1	1	1	2	1
Cyrtolobus vanduzii	1	2	1	2	2	1	1	2	1	2	3	1	1	1	2	1	2	1
Cyrtolobus vau	1	2	2	2	2	1	1	2	1	2	3	1	1	1	2	1	3	1
Glossonotus acuminatus	1	2	1	2	2	2	1	1	1	1	3	1	1	1	1	2	4	1
Glossonotus univittatus	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Godingia guerreroensis	?	2	?	2	2	1	1	2	1	2	3	1	2	1	1	1	3	1
Grandolobus grandis	1	2	1	2	2	1	1	2	1	2	3	1	1	1	2	1	3	1
Heliria cornutula	1	2	1	2	2	1	1	1	2	1	3	1	1	1	1	2	4	1
Heliria cristata	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Heliria mexicana	2	2	1	2	2	2	1	2	1	1	?	?	?	?	?	?	?	?
Heliria praealta	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Heliria scalaris	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	1	4	1
Heliria sinuata	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Helonica excelsa	1	1	1	2	2	1	1	1	1	1	3	1	1	1	1	1	4	1
Hemicardiacus saundersi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Heranice miltoglypta	1	1	1	1	?	?	?	?	?	?	3	2	1	1	1	1	1	2
Idioderma virescens	?	2	2	2	1	1	1	?	1	?	3	1	1	1	1	1	2	1
Ophiderma pubescens	1	2	1	2	2	1	2	2	1	2	3	1	1	1	2	1	3	1
Ophiderma salamandra	1	2	1	2	2	1	1	2	1	2	3	1	1	1	2	1	3	1
Palonica nogalana	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Palonica pyramidata	1	1	1	2	2	1	1	1	1	1	3	1	1	1	1	1	4	1
Palonica tremulata	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Quadrinarea perezi	1	1	1	1	?	?	?	?	?	1	2	1	1	1	?	?	3	1
Smilia fasciata	1	2	1	2	2	1	1	2	1	2	3	1	1	1	2	1	2	1
Smilirhexia naranja	?	?	?	?	?	?	?	?	?	?	3	1	1	1	1	1	3	1
Telamona ampelopsidis	2	1	1	2	2	2	1	1	1	1	3	1	1	1	1	2	4	1
Telamona balli	2	2	1	2	2	1	1	1	1	1	?	?	?	?	?	?	?	?
Telamona collina	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Telamona decorata	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Telamona extrema	1	1	1	2	2	1	1	1	2	1	2	1	1	1	1	2	4	1
Telamona gibbera	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Telamona monticola	1	2	1	2	2	2	1	1	1	1	3	1	1	1	1	2	4	1
Telamona salvini	1	2	1	2	2	1	1	2	1	1	3	1	1	1	1	1	4	1
Telamona unicolor	1	2	1	2	2	2	1	1	1	1	3	1	1	1	1	2	4	1
Telamonanthe rileyi	1	2	2	2	2	1	1	1	1	1	3	1	1	1	1	2	3	1
Telonaca alta	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	4	1
Thelia bimaculata	1	2	1	2	2	1	1	2	1	1	3	1	1	1	1	1	4	1
Thuris fenestratus	1	1	1	1	?	?	?	?	?	1	3	1	1	1	?	?	1	2
Tropidarnis tectigera	1	2	1	2	2	1	1	1	1	2	3	1	1	1	1	1	2	1

TABLE 4. (continued)

	6	6	6	6	6	6	6	6	6	7		7	7	7	7	7	7	7	7
	1	2	3	4	5	6	7	8	9	0		1	2	3	4	5	6	7	8
Xantholobus inflatus	1	2	2	2	2	1	1	2	1	2		3	1	1	1	2	1	3	1
Xantholobus muticus	2	1	2	2	2	2	1	2	1	2		3	1	1	1	1	1	2	1
Xantholobus tumidus	2	1	1	2	2	1	1	2	1	2		3	1	1	1	2	1	2	1
Ceresa vitulus	1	1	2	1	?	?	?	?	?	?		3	1	2	1	1	1	1	2
Smiliini sp. 1	?	?	?	?	?	?	?	?	?	?		3	1	1	1	2	1	2	1
Smiliini sp. 2	?	?	?	?	?	?	?	?	?	?		3	1	1	1	2	1	2	1
Spissistilus festinus	1	1	2	2	1	1	1	?	1	1		3	1	1	2	1	1	1	2
Telamonini sp.	1	2	1	2	2	1	1	1	2	1		3	1	1	1	1	1	4	1

continued.

	7	8		8	8	8	8	8	8	8	8	8	9
	9	0		1	2	3	4	5	6	7	8	9	0
Antianthe expansa	1	2		2	1	1	1	1	1	?	1	3	1&2&3&4
Antianthe foliacea	1	2		2	1	2	1	1	2	1	1	3	1&2
Archasia auriculata	1	2		1	1	3	1	2	1	?	1	3	3&4
Archasia belfragei	1	2		1	1	4	1	2	1	?	1	3	3&4
Archasia pallida	1	2		1	1	3	1	2	2	1	1	3	3&4
Ashmeadea carinata	2	1		1	1	1	1	1	1	?	2	2	2&4
Atymna castaneae	2	1		1	1	1	1	1	1	?	1	2	1&2&3&4
Atymna distincta	1	2		2	1	2	1	1	1	?	1	1	2
Atymna helena	2	2		2	2	2	2	1	?	?	1	2	3
Bryantopsis ensigera	1	2		?	1	1	2	1	1	?	1	2	1&2&3&4&5
Carynota mera	1	2		1	1	3	1	2	1	?	1	3	3&4
Cyrtolobus arcuatus	1	2		2	1	2	1	1	2	1	1	2	3&4
Cyrtolobus dixianus	1	2		2	2	2	1	1	1	?	1	2	3&4
Cyrtolobus fenestratus	1	2		2	1	2	1	1	1	?	1	2	2&3&4
Cyrtolobus inermis	1	2		2	1	2	1	1	1	?	1	1	3&4
Cyrtolobus tuberosus	2	1		1	1	2	2	1	1	?	2	3	3&4
Cyrtolobus vanduzii	2	1		1	1	2	1	1	1	?	1	2	4
Cyrtolobus vau	1	2		2	2	2	1	1	2	1	1	2	3&4
Glossonotus acuminatus	1	2		1	1	3	1	2	2	1	1	3	3&5
Glossonotus univittatus	1	2		1	1	4	1	2	1	?	1	3	3&4&5
Godingia guerreroensis	1	2		2	2	2	1	1	1	?	1	?	2
Grandolobus grandis	1	1		2	1	2	1	1	1	?	1	3	2&4
Heliria cornutula	1	2		1	1	3	1	2	1	?	1	3	3
Heliria cristata	1	2		1	1	4	1	2	1	?	1	3	2&3&4&5
Heliria mexicana	?	?		?	?	?	?	?	?	?	?	2&3	2&4
Heliria praealta	1	2		1	1	3	1	2	2	1	2	3	4&5
Heliria scalaris	1	2		1	1	4	1	2	1	?	1	3	3&4
Heliria sinuata	1	2		1	1	3	1	1	2	1	1	3	2&3&4
Helonica excelsa	1	2		1	1	4	1	2	2	1	1	3	3
Hemicardiacus saundersi	?	?		?	?	?	?	?	?	?	?	?	2

TABLE 4. (continued)

| | 7 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 9 |
	9	0	1	2	3	4	5	6	7	8	9	0
Heranice miltoglypta	1	1	?	1	1	1	1	1	?	1	3	1&2&3&4&5
Idioderma virescens	2	1	1	1	1	1	1	?	?	?	1	1&2&3&4
Ophiderma pubescens	1	2	2	2	2	1	1	2	1	1	2	3
Ophiderma salamandra	2	2	2	2	2	1	1	2	2	1	2	1&2&3&4
Palonica nogalana	1	2	1	1	4	1	2	1	?	1	3	4
Palonica pyramidata	1	2	1	1	3	1	2	1	?	1	3	2&3&4&5
Palonica tremulata	1	2	1	1	4	1	2	2	1	1	3	3&4&5
Quadrinarea perezi	?	?	?	?	1	?	1	?	?	?	1	2
Smilia fasciata	2	1	1	1	2	1	1	1	?	2	3	2&3&4
Smilirhexia naranja	1	2	2	1	4	1	?	2	1	1	?	2
Telamona ampelopsidis	1	2	1	1	4	1	2	1	?	1	3	3&4&5
Telamona balli	?	?	?	?	?	?	?	?	?	?	2	2
Telamona collina	1	2	1	1	4	1	2	2	1	1	3	3&4
Telamona decorata	1	2	1	1	3	1	2	1	?	1	3	3&4&5
Telamona extrema	1	2	1	1	3	1	2	?	?	?	3	3
Telamona gibbera	1	2	1	1	4	1	2	1	?	1	3	4
Telamona monticola	1	2	1	1	4	1	2	2	1	1	3	3&4&5
Telamona salvini	1	2	1	1	4	1	2	2	1	1	3	2&3
Telamona unicolor	1	2	1	1	4	1	2	2	1	1	3	1&3&4&5
Telamonanthe rileyi	1	2	2	1	3	1	1	2	1	1	2	3&4
Telonaca alta	1	2	1	1	4	1	2	1	?	1	3	3&5
Thelia bimaculata	1	2	1	1	3	1	1	1	?	1	3	3&4&5
Thuris fenestratus	?	?	?	?	1	1	1	?	?	?	1	1
Tropidarnis tectigera	2	2	1	1	3	1	1	2	1	1	3	2&4
Xantholobus inflatus	1	1	2	1	2	1	1	2	1	1	1	3&4
Xantholobus muticus	2	1	1	1	1	2	1	1	?	2	2	3
Xantholobus tumidus	2	1	1	1	2	1	1	1	?	2	2	3
Ceresa vitulus	?	1	1	1	1	1	1	?	?	?	2	1&2&3&4&5
Smiliini sp. 1	2	1	1	1	2	1	1	1	?	2	3	2
Smiliini sp. 2	2	1	1	1	2	1	1	1	?	2	?	2
Spissistilus festinus	?	1	?	1	1	1	1	1	?	1	2	1&2&3&4&5
Telamonini sp.	1	2	1	1	4	1	2	1	?	1	3	3

The genus *Tropidarnis* is characterized by a simple, single cucullate row of setae in row I of the metathoracic tibia (Fig. 12D). In all Smiliini *s*. Wallace, Telamonini *s*. Wallace, and *Antianthe + Hemicardiacus* specimens examined in the analysis, this row was irregular or double. Other features that distinguish it from genera in Telamonini *s*. Wallace include the absence of a median anterior pronotal horn or projection and pronotal longitudinal rugae; vein R_{4+5} in the forewing confluent with vein M basad of M fork; and a rounded, vertically oriented (from a posterior aspect; Fig. 14B, 1) style clasp with a small recurved tooth. *Tropidarnis* is found in the Neotropical and Nearctic regions (southwest United States), and both the nymphs and adults have been collected from oak (*Quercus*) (Table 2).

Geographic patterns of the *Smiliini*, *Telamonini*, and unplaced genera

The evolutionary hypothesis presented here and the optimization of geographic localities in MacClade suggests the common ancestor of the ingroup (all three clades) occurred in Central America and Mexico (Fig. 2). There were apparently multiple treehopper invasions—including the ancestors of Smiliini *s*. Wallace, and *Antianthe* group + *Tropidarnis* + Telamonini *s*. Wallace—into temperate North America, likely from Central America or southern Mexico (Fig. 2), accounting for the current Nearctic distribution of most of the ingroup. Data on geographic localities reported in the literature (Table 2; McKamey 1998) for the Smiliini *s*. Wallace and Telamonini *s*. Wallace show these two tribes are currently primarily Nearctic in distribution. First, nearly half of all treehoppers in North America are in these two tribes (Wood and Olmstead 1984; Wood and Pesek 1992; McKamey 1998). Second, 86% (n=138) of all Smiliini and Telamonini species are documented from the United States (and often Canada) and 82% (n=131) are *only* found north of Mexico (McKamey 1998). Third, only 13% (20 of 160) of Smiliini and Telamonini species combined (adjusted for removal herein of genera in Smiliinae, *incertae sedis*) are inherently tropical (South America, Central America, and Mexico) and are not documented from the United States and Canada.

While most of the ingroup taxa are currently Nearctic in distribution, the geographic location of basal and sister taxa of the three clades support a tropical origin for these treehoppers. The ancestors of both **clades one** and **two** occurred in Central America and Mexico (Fig. 2). The enigmatic taxon *Smilirhexia naranja* McKamey (**clade one**) is only known from Costa Rica. The basal lineages of **clade two**, representatives from the tribes Thuridini, Quadrinareini, Amastrini, Polyglyptini, all basal to the tribe Smiliini, are overwhelmingly tropical in their distribution. Only 20 of the 54 genera in these groups have species found in the Nearctic. Furthermore, many species in the genera *Amastris*, *Vanduzea*, *Aphetea*, and *Polyglypta* are restricted to the Neotropics (McKamey 1998). The common ancestor of the Smiliini *s*. Wallace (Fig. 2), as well as many of the ancestors of its basal lineages, inhabited Central America and Mexico. The first two lineages, *Atymna castaneae* and *Ashmeadea*, are Nearctic and Neotropical. Two notable Smiliini dispersals into temperate North America included the ancestor of the clade including *Cyrtolobus tuberosus* and the ancestor of the large clade including *Godingia*, *Ophiderma* and various *Atymna* and *Cyrtolobus* spp. Indeed, 84% (n=77) of the Smiliini are found primarily north of Mexico (some species have slightly overlapping temperate and tropical distribution) while 16% (n=15) of the Smiliini are only found in the tropics (McKamey 1998).

The common ancestor of **clade three** and the clade *Tropidarnis* + Telamonini originally occupied Central America and Mexico (Fig. 2). Species from the *Antianthe* group and *Tropidarnis* are primarily Neotropical (Table 2). Although the ancestral distributions of the Telamonini *s*. Wallace and several smaller terminal clades within the tribe are equivocal, the ancestor of a large group, including most telamonine species, inhabited the United States (Fig. 2). Ninety-three percent (n=63) of the Telamonini are found primarily north of Mexico (some species have slightly overlapping temperate and tropical distributions), while only 7% (n=5) are restricted to the tropics (McKamey 1998).

When examining generic trends of the Smiliini *s*. Wallace and Telamonini *s*. Wallace in the United States, the central and eastern and southwestern U. S. appear to be "hotspots." All Smiliini genera and nine of ten Telamonini genera have species in the southwestern U. S. or Mexico. All Telamonini genera and five of nine Smiliini genera are documented from the central and eastern U.S. Only the Telamonini, however, have genera (50%) in the Pacific Northwest. The high diversity of both Smiliini and Telamonini in the southwestern U. S. and its close proximity to the tropics, helps corroborate a Neotropical origin for the Smiliini and Telamonini, subsequently followed by a dispersal and radiation north and east into temperate North America. Indeed, Wood and Olmstead (1984) postulated that a Smiliini *s.l.* progenitor likely arose in the Mexican Highlands. Cast (2002), based on phylogenies revealing southwestern U.S. Smiliini lineages and Panama Telamonini lineages basal to their respective North American fauna, hypothesized a Central American highland origin with subsequent dispersal and geographic regionalization of the Smiliini and Telamonini into North America.

Host plant families

The *Smiliini s*. Wallace, *Telamonini s*. Wallace, *Antianthe* group, and *Tropidarnis* are known from at least 14 plant families based on host plant accounts in the literature (Table 2). Despite their apparent polyphagous habit, many

species within these lineages are specialists on oak (Fagaceae: *Quercus*), having been collected from approximately 30 different oak species. Indeed, Wood and Olmstead (1984) stated that 106 of 156 Smiliini species *s.l.* are only on oak and referred to them as oak specialists. A review of the literature for this study revealed that 90 (two of these only reported at the genus level) of the 169 species from these four lineages (Smiliini, n=51; Telamonini n=37; *Antianthe* group, n=1; *Tropidarnis* n=1) have been collected on various oak species, while one Smiliini species, *Atymna castaneae* is a specialist on a close relative, chestnut (Fagaceae: *Castanea dentata*). The number of species known from oak is likely underestimated because only accounts from the literature and not from specimen labels are reported here. Recent ecological studies in eastern Pennsylvania suggest some oak-feeding treehoppers are even more highly specialized, feeding on mostly oak species in either the red or white oak group (Wallace and Troyano 2006; Wallace 2008). Of the 46 species from these groups reported from non-Fagaceae families, 32 have also been found on oak, so it is possible that collections on plants other than oaks were results of "temporary stopovers". Additionally, in many cases, host plants reported in the literature can only be defined as "host associations," because only the adult was collected without the immature (primary feeding life stage). Nevertheless, 12 species, all Telamonini *s.* Wallace, are only known from families other than Fagaceae: Betulaceae, Fabaceae, Platanaceae, Rosaceae, Salicaceae, Ulmaceae, Tiliaceae, and Vitaceae. Although Ball (1931) and Deitz (1975) noted that both the Smiliini *s.s.* and Telamonini *s.l.* are strictly tree feeders and other Smiliinae are restricted to herbaceous plants, this host data emphasizes the distinctiveness of the Telamonini *s.* Wallace from the Smiliini *s.* Wallace and helps corroborate the monophyly of each in the present analysis (Fig. 1). Cast (2002) used similar host plant information to support a comparable classification scheme.

It is premature to hypothesize an ancestral plant family for the current ingroup until more genera of Smiliinae and their host plants are included in an analysis. Moreover, there remains a large amount of missing and putative host plant data in regards to numerous ingroup taxa. Although some Polyglyptini, Ceresini, and Amastrini have been reported on oak, many species within these groups appear to be quite polyphagous (Amastrini and Polyglyptini are found on at least over 15 plant families each), commonly found on the plant families Asteraceae and Fabaceae, and none are specialists on oak. Yet, the evolutionary hypothesis and host plant data (large number of oak specialists) presented here suggest that the immediate ancestors to the Smiliini *s.* Wallace and Telamonini *s.* Wallace were probably oak feeders, or at least, early on in Smiliini and Telamonini evolution there was a switch to Fagaceae from another plant family. McKamey (2008) suggested *Smilirhexia*, based on its locality in an oak upland, likely feeds on oak. Two of the basal genera of **clade three**, *Hemicardiacus* (*Antianthe* group) and *Tropidarnis*, are reported from oak (Table 2).

As a result of their discriminate function analysis of the membracid pronotum, Wood and Pesek (1992) suggested Fabaceae was the ancestral host plant of the Smiliini *s.l.* because *Thelia bimaculata* (only on black locust) was located at the base of their tree. In Cast's (2002) phylogeny based on mitochondrial DNA, *Thelia*, *Carynota*, and *Glossonotus crataegi* were basal lineages in the Telamonini. All are non-oak feeders, providing Cast independent evidence for these taxa as historic lineages. In the phylogeny presented here, however, *Thelia* is quite derived, and the other species in the genus (*Thelia uhleri* Stål) is known from other plant families, notably the Rosaceae.

Cast (2002) concluded the common ancestor of Smiliini and Telamonini likely colonized oak, leading to radiation and dispersal of these treehoppers throughout central and North America. Wood and Pesek (1992) also stated that following a switch to oak as the primary host plant, the Smiliini *s.l.* radiated extensively. Based on the phylogeny presented here, such a radiation may have occurred twice—in the Smiliini *s.* Wallace and the Telamonini *s.* Wallace—both of which contain many oak specialists. The presence of telamonine species on plants other than oak suggests their ancestors switched from oak to various other hardwoods in the oak-hickory forest (such as apple, plum, willow, aspen, basswood, and sweetgum), perhaps as a behavioral response to increased competition. Notable among these non-oak hosts is the family Rosaceae, from which no Smiliini are reported, providing independent evidence of the distinctiveness of the Telamonini.

Phylogeny, geographical patterns, and host plants: clues to a geographic origin?

Based on the results of this study (discussed above) and others (Wood and Pesek 1992; Cast 2002), it appears the Smiliini *s.* Wallace, Telamonini *s.* Wallace, *Antianthe* group, and *Tropidarnis* treehoppers likely originated in Central America or southern Mexico and subsequently underwent extensive radiation, along with their primary host

Quercus, during at least two separate dispersal events north into temperate North America. Based on other similar phylogenetic studies on membracids and the present analysis, it is reasonable to hypothesize that these tribes originated and began their northern dispersal between 30-5 MYA. Results of recent molecular and morphological phylogenetic studies and the scant treehopper fossil record (Dietrich *et al.* 2001a; Dietrich *et al.* 2001b; Wallace and Deitz 2004, 2006; Cryan *et al.* 2004; Grimaldi and Engel 2005) suggest that the earliest membracid lineages arose during the Tertiary period in the Neotropics, perhaps 57.8–5.3 million years ago. Given the relatively derived position of the selected Smiliini, Telamonini, *Antianthe* group, and *Tropidarnis* in evolutionary analyses of the family (Dietrich *et al.* 2001a; Cast 2002; Cryan *et al.* 2004), these taxa are likely recently derived, diversifying much less than 57 million years ago. Indeed, Wood and Pesek (1992) speculated that the Smiliini *s.l.* are less than 65 million years old, colonizing North America in the last five million years.

Comparing the results of the treehopper evolutionary studies cited above with the findings of biogeographical research on oaks and related plants (Manos and Stanford 2001) hints toward a close evolutionary relationship between North American oaks and treehoppers. Indeed, oak diversity is highest in Central and North America, similar to the diversity of the treehoppers in this study (Wood and Pesek 1992; Manos and Stanford 2001). Studies show that the North American Fagaceae were relatively diversified by the early Tertiary, with foci in the Nearctic, Southern Mexico, and Central and South America. The minimum age of the family is hypothesized at 65-45 MYA (Upper Paleocene to Lower Eocene). Modern *Quercus* (oak) were likely present in the upper Eocene to lower Oligocene (55-25 MYA) (Manos and Stanford 2001).

The hypothesized diversification of oak, therefore, roughly coincides with the hypothesized diversification of the Smiliini, Telamonini, *Antianthe* group, and *Tropidarnis* treehoppers, suggesting possible coevolution between oak and these taxa. The results of this analysis independently support Wood and Pesek's (1992) statement that the Smiliini *s.l.* diversified after "colonizing *Quercus*". These authors also speculated that because few other treehoppers worldwide are found on oak, the colonization to oak by the Smiliini is a recent one, further supporting a recent origin for these taxa. Other insects have similar relationships with oak. Leaf-mining lepidopterans and gall-forming cynipid wasps have both been associated with oaks for over 20 million years (Grimaldi and Engel 2005). These oak-feeding treehoppers are yet another example of this close evolutionary association.

Wood and Olmstead (1984) also hypothesized that the ancestor of the Smiliini *s.l.* became specialized on oak in the region of the Mexican highlands, the proposed center of oak diversity. Furthermore, they suggested that speciation in the Smiliini *s.l.* may have occurred in a similar way to *Enchenopa binotata*, through host specialization. The various phenologies of North American oaks would support treehopper specialization and diversification on different oak species via temporal isolation (Wood and Olmstead 1984). Cast (2002) stated that advancing glaciers and colder, drier climates resulted in isolation of oaks and treehoppers followed by geographic regionalization and extensive radiation of both taxa.

The shapes of the pronotal hood in species from these groups also support a close relationship with their oak hosts. The pronotum of many species, especially in the Smiliini *s.* Wallace and Telamonini *s.* Wallace, resemble various plant parts, such as buds (*Cyrtolobus*, *Ophiderma*, *Telamona*, *Heliria*), fresh or weathered leaf fragments (*Antianthe*, *Archasia*, *Tropidarnis*), or broken twigs (*Glossonotus*, *Heliria*, *Telonaca*). The wide variety of these shapes, evident in adults and nymphs, suggests that the pronotum may be an adaptation for protection from predators, by closely mimicking inanimate objects of no concern to predators. Other authors have (Funkhouser 1917; Deitz 1974; Wood 1993) also suggested crypsis as a possible function of the treehopper pronotum. These adaptations, therefore, may be a product of their evolution in North America.

Concluding remarks

Results of the first comprehensive phylogenetic analysis of the treehopper tribe Smiliini *s.l.* based on morphology indicate the tribe, as most recently defined, is not likely monophyletic. This analysis supported a revised classification with two tribes: the Smiliini *s.* Wallace and Telamonini *s.* Wallace (Table 2). The phylogenies presented by Cast (2002) support these findings and classification changes. Although at many nodes of the tree Bremer support and character changes were relatively low, several characters—including aspects of the pronotum, wing venation, and male and female genitalia—were critical in elucidating evolutionary relationships and delimiting these tribes.

Tribal revisions of the Smiliini and the Telamonini, including nymphs when available, are needed to clarify the morphological limits of the genera and species. Thus, although there are sufficient characters to support these

tribes, more characters and taxa are needed to test the phylogeny proposed here. An in-depth analysis of the entire subfamily Smiliinae, including many more tribal representatives (notably in Acutalini, Micrutalini, and Tragopini) is needed to confirm these present findings, to determine the evolutionary relationships among the Smiliinae tribes, and to make informed decisions about the limits of genera. It is hoped that characters shown in this analysis, along with new nymphal characters, will form a sound foundation for solidifying generic concepts in future studies of the individual tribes.

TABLE 5. Specimens examined.

The codens following the taxa below refer to the following institutions: ESUC, East Stroudsburg University Insect Collection, East Stroudsburg, PA; FSCA, Florida State Collection of Arthropods, Gainesville, FL; INBio, Instituto Nacional de Biodiversidad, Santa Domingo de Heredia, Costa Rica; NCSU, North Carolina State University Insect Museum, Raleigh, NC; UDCC, University of Delaware Insect Collection, Newark, DE; USNM, National Museum of National History, Washington, D.C. Tribal names follow the present reclassification based on the phylogenetic analysis (*s*. Wallace).

Identified taxa used in the analysis (alphabetized by genus and species):

Antianthe expansa (Germar) (Smiliinae *incertae sedis*) (NCSU, USNM); *A. foliacea* (Stål) (Smiliinae *incertae sedis*) (USNM); *Archasia auriculata* (Fitch) (Telamonini) (NCSU); *A. belfragei* Stål (Telamonini) (ESUC); *A. pallida* (Fairmaire) (Telamonini) (NCSU); *Ashmeadea carinata* (Stål) (Smiliini) (USNM): *Atymna castaneae* (Fitch) (Smiliini) (ESUC); *A. distincta* Plummer (Smiliini) (USNM); *A. helena* (Woodruff) (Smiliini) (ESUC); *Bryantopsis ensigera* Ball (Polyglyptini) (USNM); *Carynota mera* (Say) (Telamonini) (ESUC); *Ceresa vitulus* (Fabricius) (Ceresini) (USNM; *Cyrtolobus arcuatus* (Emmons) (Smiliini) (ESUC); *C. dixianus* Woodruff (Smiliini) (ESUC); *C. fenestratus* (Fitch) (Smiliini) (ESUC); *C. inermis* (Emmons) (Smiliini) (ESUC); *C. tuberosus* (Fairmaire) (Smiliini) (ESUC); *C. vanduzii* (Goding) (Smiliini) (USNM); *C. vau* (Say) (Smiliini) (ESUC); *Glossonotus acuminatus* (Fabricius) (Telamonini) (ESUC); *G. univittatus* (Harris) (Telamonini) (ESUC); *Godingia guerreroensis* Fowler (Smiliini) (USNM); *Grandolobus grandis* (Van Duzee) (Smiliini) (USNM); *Heliria cornutula* Ball (Telamonini) (NCSU); *H. cristata* (Fairmaire) (USNM); *H. mexicana* (Stål) (Telamonini) (USNM); *H. praealta* (Fowler) (Telamonini) (USNM); *H. scalaris* (Fairmaire) (Telamonini) (UDCC); *H. sinuata* (Fowler) (Telamonini) (USNM); *Helonica excelsa* (Fairmaire) (Telamonini) (ESUC, USNM); *Hemicardiacus saundersi* Plummer (holotype) (Smiliinae *incertae sedis*) (USNM); *Heranice miltoglypta* (Fairmaire) (Polyglyptini) (USNM); *Idioderma virescens* Van Duzee (Amastrini) (USNM); *Ophiderma pubescens* (Emmons) (Smiliini) (ESUC); *O. salamandra* Fairmaire (Smiliini) (ESUC); *Palonica pyramidata* (Uhler) (Telamonini) (USNM); *P. nogalana* Ball (Telamonini) (USNM); *P. tremulata* (Ball) (Telamonini) (USNM); *Quadrinarea perezi* Ramos (Quadrinareini) (USNM); *Smilia fasciata* Amyot and Serville (Smiliini) (ESUC); *Smilirhexia naranja* McKamey (holotype) (Smiliinae *incertae sedis*) (INBio); *Spissistilus festinus* (Say) (Ceresini) (ESUC); *Telamona ampelopsidis* (Harris) (Telamonini) (ESUC, USNM); *T. balli* Plummer (Telamonini) (USNM); *T. collina* (Walker) (Telamonini) (ESUC, NCSU); *T. decorata* Ball (Telamonini) (ESUC); *T. extrema* Ball (Telamonini) (ESUC); *T. gibbera* Ball (Telamonini) (NCSU); *T. monticola* (Fabricius) (Telamonini) (ESUC); *T. salvini* Distant (Telamonini) (ESUC, USNM); *T. unicolor* Fitch (Telamonini) (ESUC); *Telamonanthe rileyi* (Goding) (Telamonini) (USNM); *Telonaca alta* (Funkhouser) (Telamonini) (USNM); *Thelia bimaculata* (Fabricius) (Telamonini) (ESUC, NCSU); *Thuris fenestratus* Funkhouser (Thuridini) (USNM); *Tropidarnis tectigera* (Fowler) (Smiliinae *incertae sedis*) (USNM); *Xantholobus inflatus* (Van Duzee) (Smiliini) (USNM); *X. muticus* (Fabricius) (Smiliini) (ESUC); *X. tumidus* (Walker) (Smiliini) (ESUC).

Unidentified taxa used in the analysis:
Smiliini sp. 1 (Smiliini) (FSCA); Smiliini sp. 2 (Smiliini) (FSCA); Telamonini sp. 1 (Telamonini) (UDCC).

Other specimens examined:
Atymna gigantea Plummer (Smiliini) (USNM); *A. querci* (Fitch) (Smiliini) (ESUC); *A. simplex* (Van Duzee) (Smiliini) (USNM); *Bajulata bajula* (Goding) (Amastrini) (USNM); *Carynota marmorata* (Say) (Telamonini) (USNM); *C. stupida* (Walker) (Telamonini) (USNM); *Cyrtolobus distinguendus* Fowler (Smiliini) (USNM); *C. flavolatus* Woodruff (Smiliini) (NCSU); *C. fuliginosus* (Emmons) (Smiliini) (ESUC); *C. funkhouseri* Woodruff (Smiliini) (ESUC); *C. fuscipennis* Van Duzee (Smiliini) (ESUC); *C. maculifrontis* (Emmons) (Smiliini) (ESUC); *C. ovatus* Van Duzee (Smiliini) (ESUC); *C. pallidifrontis* (Emmons) (Smiliini) (ESUC); *Glossonotus crataegi* (Fitch) (Telamonini) (ESUC); *G. nimbatulus* Ball (Telamonini) (ESUC); *Heliria fitchi* Ball (Telamonini) (ESUC, USNM); *H. molaris* (Butler) (Telamonini) (USNM); *H. strombergi* Goding (Telamonini) (FSCA, USNM); *Ophiderma definita* Woodruff (Smiliini) (ESUC); *O. evelyna* Woodruff (Smiliini) (ESUC); *O. flavicephala* Goding (Smiliini) (ESUC); *Smilia camelus* (Fabricius) (Smiliini) (ESUC); *Telamona archboldi* Froeschner (Telamonini) (USNM); *T. compacta* Ball (Telamonini) (ESUC); *T. concava* Fitch (Telamonini) (ESUC, NCSU); *T. maculata* Van Duzee (Telamonini) (ESUC, USNM); *T. reclivata* Fitch (Telamonini) (ESUC); *T. tiliae* Ball (Telamonini) (USNM); *T. tristis* Fitch (Telamonini) (NCSU, USNM); *T. westcotti* Goding (Telamonini) (NCSU); *Telamonanthe pulchella* (Ball) (Telamonini) (USNM); *Thelia uhleri* Stål (Telamonini) (ESUC, USNM); *Vanduzea arquata* (Say) (Amastrini) (ESUC); *Xantholobus intermedius* (Emmons) (Smiliini) (ESUC); *X. lateralis* (Van Duzee) (Smiliini) (NCSU); *X. nitidus* (Van Duzee) (Smiliini) (NCSU).

TABLE 6. List of Bremer support values and apomorphies for the phylogenetic analysis (Fig. 1). Bremer support values are indicated in parentheses following the node number. Characters are listed with states in parentheses; non-homoplastic changes are marked by an asterisk (*).

Node 175 (3+)	40(1), 51(2)*, 54(2), 65(2), 77(3), 78(1), 80(2), 86(2)
Node 174 (2)	14(2)*, 28(2), 35(2), 37(2)*, 44(2)*, 56(2)
Node 173 (2)	4(2), 18(2), 20(2), 21(2), 27(2), 32(2), 38(1), 60(2), 89(3)
Node 172 (1)(Telamonini)	62(2), 63(1), 68(1), 83(3)
Node 171 (2)	17(2), 30(2), 33(2), 41(2), 76(2)
Node 170 (3+)	36(2), 45(2)*, 53(1), 81(2), 89(2)
Node 169 (1)	61(2)
Node 168 (2)	2(2), 3(1), 46(2), 77(4), 85(2)
Node 167 (2)	5(2), 11(2), 25(3)
Node 166 (2)	49(2)*, 86(1)
Node 165 (1)	27(1), 57(2)
Node 164 (1)	26(2)*, 83(4)
Node 163 (1)	20(1)
Node 162 (1)	23(2)*
Node 161 (1)	57(1)
Node 160 (1)	18(1), 83(3), 86(2)
Node 159 (1)	21(1), 28(1)
Node 158 (1)	33(1), 86(1)
Node 157 (1)	20(1), 25(2)
Node 156 (1)	33(1)
Node 155 (1)	18(1)
Node 154 (1)	60(1), 83(4)
Node 153 (1)	86(2)
Node 152 (3+)	5(3), 19(1), 66(2)
Node 151 (1)	18(2), 33(2)
Node 150 (1)	24(2)*
Node 149 (1)	27(1)
Node 148 (1)	62(1)
Node 147 (1)	34(2)
Node 146 (1)	11(1), 12(2), 17(1)
Node 145 (1)	15(2)
Node 144 (1)	30(1)
Node 143 (1)	1(1), 12(2), 15(2), 33(3), 81(2)
Node 142 (2)	2(2), 35(1), 38(2), 43(2)
Node 141 (2)	31(2)*, 39(1), 43(2), 53(1), 80(1), 86(1)
Node 140 (2)	33(2), 46(2), 62(2), 70(2), 77(2), 79(2)
Node 139 (1)(Smiliini)	39(2), 47(1)
Node 138 (2)	7(2), 8(2), 9(2), 13(1), 88(2)
Node 137 (1)	83(2)
Node 136 (1)	28(3), 61(2), 84(2)
Node 135 (1)	52(2), 62(1)
Node 134 (2)	7(1), 63(1), 75(2), 84(1)
Node 133 (1)	63(1), 75(2)
Node 132 (2)	8(1), 15(2), 89(3)
Node 131 (1)	88(1)
Node 130 (2)	77(3), 79(1), 81(2)
Node 129 (1)	80(2)
Node 128 (1)	63(2)
Node 127 (1)	13(2), 82(2)
Node 126 (1)	6(2), 86(2)
Node 125 (2)	9(1), 10(1), 34(2), 52(2)
Node 124 (3+)	7(1), 16(1), 63(1)
Node 123 (1)	28(3), 75(1)
Node 122 (1)	9(1)
Node 121 (2)	7(1), 35(1), 67(2)
Node 120 (1)	67(2)
Node 119 (2)	58(1)*, 63(1), 64(1)
Node 118 (2)	30(2), 36(2), 38(1), 59(2)*
Node 117 (2)	3(3), 40(2), 54(1), 89(1)

Ceresa vitulus/S. festinus	43(2), 64(1), 73(2)
Smilirhexia naranja	1(1), 3(1), 10(1), 41(2), 50(1), 81(2), 83(4)
Quadrinarea perezi	2(2), 8(2), 10(1), 16(1), 28(1), 56(1), 71(2)
Thuris fenestratus	1(1), 6(2), 9(2), 35(1), 41(2), 51(1)*, 77(1), 78(2)
Heranice miltoglypta	4(2), 32(2), 39(2), 77(1), 78(2), 89(3)
Bryantopsis ensigera	1(1), 17(2), 28(1), 56(1), 80(2), 84(2)
Idioderma virescens	10(1), 16(1), 35(1), 40(3), 54(1), 65(1), 89(1)
Atymna castaneae	75(2)
Ashmeadea carinata	46(1), 56(1)
Cyrtolobus tuberosus	89(3)
Xantholobus muticus	66(2), 83(1)
Xantholobus tumidus	8(1)
Smiliini sp. 2	11(2), 13(2), 46(1)
Smilia fasciata	42(2)
Smiliini sp. 1	3(1), 9(1), 32(2), 43(1), 47(2), 52(2), 57(2)
Cyrtolobus vanduzii	42(2), 50(1)
Grandolobus grandis	35(1), 89(3)
Cyrtolobus arcuatus/	68(1), 69(2), 86(2)
Cyrolobus fenestratus	
Atymna distincta	35(1), 89(1)
Cyrtolobus dixianus	--
Godingia guerreroensis	13(1), 52(2), 73(2)
Cyrolobus inermis	34(2), 82(1), 89(1)
Atymna helena	63(1), 68(1), 79(2), 84(2)
Cyrtolobus vau	--
Xanthlobus inflatus	6(1), 46(1), 80(1), 82(1), 89(1)
Ophiderma salamandra	79(2)
Ophiderma pubescens	60(2)
Hemicardiacus saundersi	3(1), 41(2)
Antianthe expansa	61(2), 66(2), 86(1)
Antianthe foliacea	83(2)
Tropidarnis tectigera	35(1), 54(1), 60(1), 70(2), 77(2), 79(2)
Telamonanthe rileyi	63(2)
Heliria mexicana	66(2), 68(2)
Telamona balli	--
Telamona salvini	68(2), 76(1), 83(4)
Heliria sinuata	85(1)
Heliria cornutula	69(2)
Heliria scalaris	18(1), 76(1)
Heliria cristata	--
Telamonini sp.	19(1), 25(2), 28(1), 69(2), 76(1)
Telonaca alta	2(1), 52(2)
Heliria praealta	88(2)
Glossonotus acuminatus	18(2), 66(2)
Glossonotus univittatus	19(1), 34(2), 83(4)
Thelia bimaculata	68(2), 76(1), 85(1)
Palonica pyramidata	62(1), 76(1)
Telamona decorata	5(3)
Carynota mera	8(2), 10(1)
Archasia pallida	60(1), 86(2)
Archasia auriculata	5(1)
Archasia belfragei	66(2), 69(2), 83(4)
Telamona extrema	19(1), 30(1), 62(1), 69(2), 71(2)
Telamona gibbera	--
Telamona unicolor	--
Telamona monticola	--
Palonica tremulata	--
Palonica nogalana	5(1), 86(1)
Telamona collina	5(3)
Helonica excelsa	76(1)
Telamona ampelopsidis	61(2), 66(2), 86(1)

Acknowledgments

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